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Notes on the Taxonomy and Growth Habits of Three Species of *Campyloneurum* (Polypodiaceae) from Southeastern Brazil

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Abstract.—Among the *Campyloneurum* that occur entirely or primarily in the Atlantic Rain Forest of Brazil, three species have been previously referred to by the following six names: *C. acrocarpon, C. crispum, C. herbaceum, C. lapathifolium, C. minus,* and *C. wacketii.* We show that *C. crispum* and *C. herbaceum* are the correct names for two of the species, and we designate lectotypes for these two names. The third species, which ranges from Brazil to Argentina and Paraguay, lacks a name and is here newly described as *C. atlanticum.* Two of the previously used names, *C. acrocarpon* and *C. wacketii,* are considered synonyms of *C. crispum.* The remaining names, *C. lapathifolium* and *C. minus,* appear to be of uncertain application. Based on our field studies, *C. atlanticum* and *C. herbaceum* are primary hemiepiphytes. Our finding constitutes the first report of this growth habit in the genus. The third Brazilian species treated herein, *C. crispum,* varies in growth habit, being either terrestrial, primary hemiepiphytic, or holoepiphytic. The spores of the three species are uniform and typical of the genus; they do not provide any distinguishing characters for the species.

Key Words.—Atlantic Rain Forest, diversity, eupolypods, ferns, hemiepiphytism, pteridophyte

Campyloneurum C. Presl contains about 60 species (pers. obs.) and is entirely Neotropical (Lellinger, 1988; Tryon and Tryon, 1982). It forms a clade with *Microgramma* C. Presl and *Nipihidium* J. Sm., but the exact sister relationship of *Campyloneurum* to these two genera is not well resolved. Schneider et al. (2004), Kreier et al. (2007), and Salino et al. (2008) recovered

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Campyloneurum as sister to *Niphidium*, but Schuettpelz and Pryer (2007) recovered it as sister to *Microgramma*. In these studies, however, phylogenetic support values were low.

Campyloneurum, Microgramma, and *Niphidium* share several characters in common. All have simple and entire leaves, except for a clade of three 1-pinnate species formed by *C. decurrens* C. Presl, *C. magnificum* T. Moore, *C. pentaphyllum* (Willd.) Pic. Serm. The three genera also have anastomosing venation with included veinlets in the areoles. Prominent lateral veins run from the costa to the lamina margin in *Niphidium* (Lellinger, 1972) and in most species of *Campyloneurum,* but such veins are absent in *Microgramma* (de la Sota and Pérez-García, 1982). Between the main lateral veins of *Niphidium* occur secondary finer veins that are somewhat irregularly reticulate. In contrast, *Campyloneurum* typically has the secondary veins forming an arc between the main lateral veins, and these arced secondary veins typically bear two excurrent veinlets.

Campyloneurum is represented in Brazil by 22 species, six of which are endemic (Labiak and Hirai, 2016). Thirteen species occur in the Atlantic Rain Forest of southeastern and southern Brazil, with some of them also reaching the western part of Paraguay and Argentina following the inland expansion of the Atlantic Rain Forest in Paraná and Santa Catarina states. Although some studies have dealt with the taxonomy of *Campyloneurum* in Brazil (e.g., Sehnem, 1970; Lellinger, 1988; Vasques and Prado, 2011; Labiak and Hirai, 2016), our ongoing molecular phylogenetic study on *Campyloneurum* has shown that some taxonomic problems still exist. This paper focuses on one of those problems, which concerns the taxonomy of three species of *Campyloneurum* endemic to the Atlantic Rain Forest of Brazil and northeastern Argentina and Paraguay. These species have been previously referred to by six names, in both the literature (e.g., Vasques and Prado, 2011; Labiak and Hirai, 2016) and as identifications on herbarium specimens: *C. acrocarpon* Fée, *C. crispum* Fée, *C. herbaceum* (Christ) Ching, *C. lapathifolium* (Poir.) Ching, *C. minus* Fée, and *C. wacketii* Lellinger. Our paper also examines the growth form of the three species. Two of the species have slender long-creeping rhizomes that climb trunks (Figs. 1, 2). It seemed likely that they represent primary hemiepiphytes sensu Benzing (2008), a growth form that has not yet been documented in *Campyloneurum*. Our paper 1) evaluates the types of the six names and determines how to apply them, and 2) examines the two putatively primary hemiepiphytic species in the field, to determine their growth habits.

MATERIALS AND METHODS

Type specimens of the five names were studied at MO and P, and from on-line images available on JSTOR Global Plants. The specimens examined for the three species were compiled from the collections at MBM, MO, NY, P, and UPCB. Also, we investigated specimen images available on the Reflora Project website (www.reflora.jbrj.gov.br). In the list of specimens we present only two specimens per state or department. An index to collectors' names and number

(Appendix 1) includes not only those in the specimens examined sections, but also all others examined for this study. In the descriptions of the three species, the largest leaf on each specimen was measured for length and width. Field studies were carried out by two of us (Matos and Labiak) in the Brazilian states of Paraná, São Paulo, and Rio de Janeiro to document growth habit. Multiple plants were observed to determine whether gametophytes and rhizomes began growth on the ground or on trunks. Also, plants in the field were examined as to whether feeding roots (sensu Lagomarsino et al., 2012) were present and, for plants on tree trunks, how high up on the trunk the rhizomes began growth. In order to examine the perine ornamentation, SEM images of the spores were obtained using a JEOL JSM-5410LV scanning electron microscope, following the protocols of Moran et al. (2010).

Results and Discussion

Taxonomy.—Based on our studies of the types for *Campyloneurum acrocarpon, C. lapathifolium*, and *C. minus,* we conclude that none of them apply to the species that occur in the Atlantic Rain Forest of Brazil. Instead, we found that two overlooked names, *C. crispum* Fée and *C. herbaceum* (Christ in Schwacke) Ching, do apply and should be used. One of the three species lacks a valid name; accordingly, it is described as new herein.

The spores of the three species were very similar to each other in terms of sizes and perine ornamentation (Fig. 3) and to other species in the genus, such as those illustrated by Tryon and Tryon (1982) and Tryon and Lugardon (1991). Because of their great similarity, they do not provide any characters to distinguish the species within *Campyloneurum*.

Specific comments on each species are provided below, as well as lectotypifications when necessary.

Campyloneurum atlanticum R. C. Moran & Labiak, **sp. nov.** Type: Brazil. **Paraná**: Mun. Quatro Barras, Serra da Graciosa, Morro Mãe Catira, 25°20′20″S, 48°54′37″W, 970 m, 1 Feb 2016, *F. B. Matos, C. R. Royer, L. C. de Lannoy & L. K. Hinoshita 2548* (holotype: UPCB; isotypes: NY, P, RB). (Fig. 1 A–C, H, K, and Fig. 2 A–C.)

Diagnosis.—Plants primary hemiepiphytic or epipetric; rhizomes long creeping, with ovate, slightly bullate and light castaneous to orangish. This species differ from *C. herbaceum* by wider laminae (2.0–4.3 cm vs. 1.6–2.8 cm) and longer petioles (3.5–10.0 vs. 0.5–3.0 cm). Also distinct from *C. crispum,* which has longer leaves (up to 1.2 m long vs. 52 cm), wider laminae (4.3–8.0 cm vs. 2.0–4.3 cm), and short and compact rhizomes.

Plants hemiepiphytic or epipetric. Rhizomes long creeping, 2–4 mm wide; rhizome scales 1.0–1.5 mm long, ovate, slightly bullate, orange to orange-brown, cells more or less isodiametric, irregular. Leaves 21.0–51.5 cm long; petioles 3.5–10.0 cm, ratio to leaf length 3.1–9.7; laminae 2.0–4.3 cm wide,

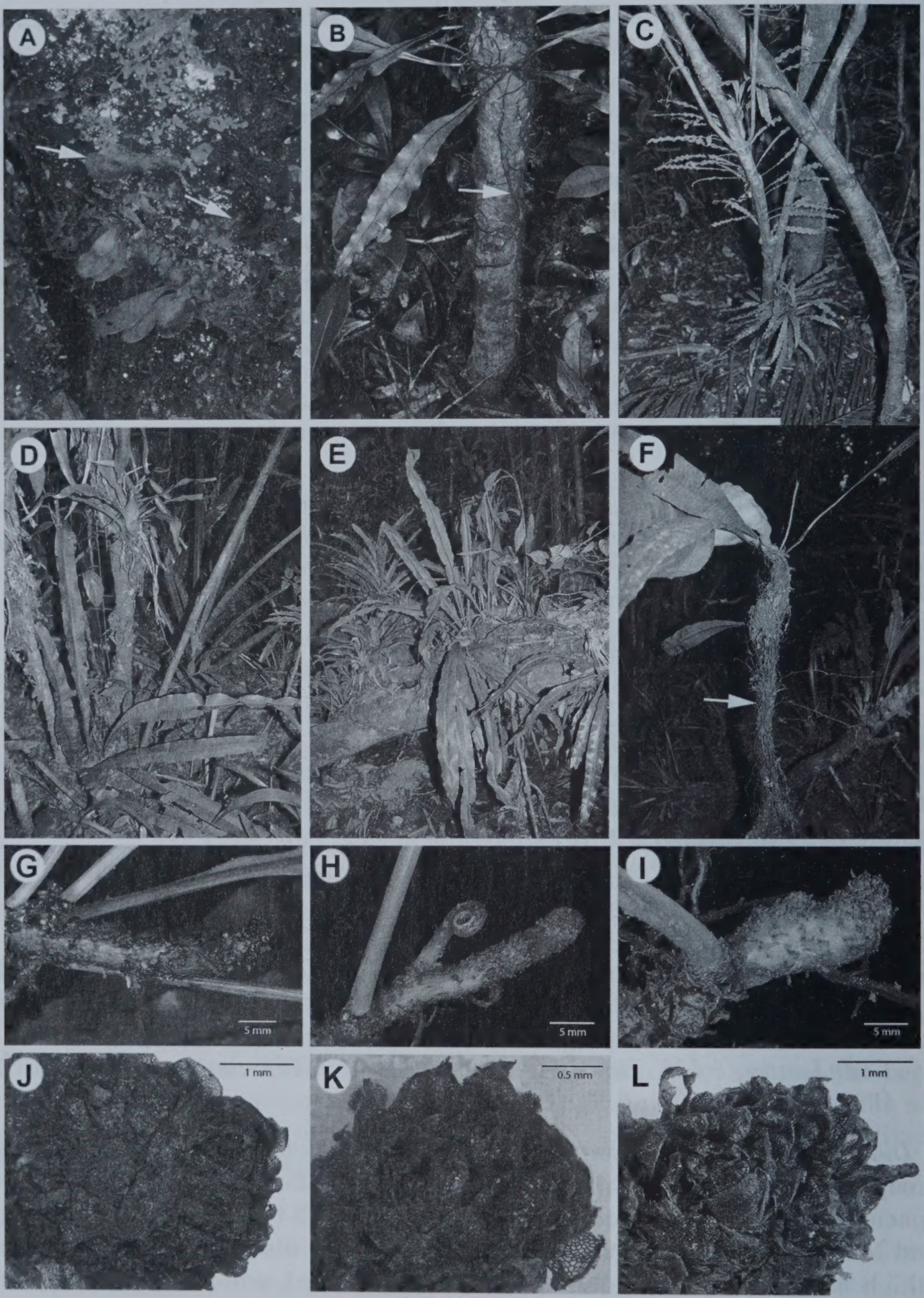

FIG. 1. A–L. Growth habit, rhizomes, and rhizome scales of three species of *Campyloneurum* endemic (or nearly so) to southeastern Brazil. **A.** *C. atlanticum,* Gametophytes (arrows) and first sporeling leaves as holoepiphytes on base of trunk. **B.** *C. atlanticum,* primary hemiepiphyte on base of trunk, with a long feeding root (arrow) descending to soil. **C.** *C. herbaceum,* primary hemiepiphyte starting around base of trunk. **D.** *C. crispum,* terrestrial plant. **E.** *C. crispum,*

narrowly lanceolate, short-decurrent at the base, acuminate at the apex; sori in (4–)6–8(–9) rows between the costa and the margin.

Specimens examined.—**ARGENTINA. Misiones**: Depto Cainguás, Ruta 7, 2 km W del acceso a Aristóbulo del Valle, 27°07′00″S, 54°55′00″W, 28 Jul 1987, *Vanni et al. 781* (MO); Depto Eldorado, Ruta Prov 17, 72 km de Dos Hermanas camino a Eldorado, 26°23′S, 54°14′W, 14 Oct 1996, *Morrone et al. 1329* (MO); Depto San Pedro, Parque Provincial Piñalito, Arroyo Sidra, 26°25′S, 53°50′W, 750 m, 11 Mar 2002, *Múlgura de Romero et al. 3240* (MO); Depto San Pedro, Parque Provincial Piñalito, sendero hacia el Arroyo Sidra, 26°26′S, 53°50′W, 06 Mar 2000, *Deginani et al. 1732* (MO); Depto Oberá Salto Krisiuk, 27°29′S, 55°08′W, 42042, *Cabral et al. 707* (NY).

BRAZIL. Bahia: Jussari, RPPN Serra do Teimoso. Rodovia Jussari-Palmira. Fazenda Teimoso, entrada à esquerda ca. 7,5 Km de Jussari, trilha para o topo da serra, 15°09′37″S, 39°32′10″W, 27 Jul 2005, *Matos et al. 784* (UPCB). **Espírito Santo**: Castelo, Parque Estadual do Forno Grande, afloramentos rochosos com matas úmidas nos vales, 20°31′16″S, 41°05′50″W, 1700 m, 18 Jul 2007, *Labiak et al. 4229* (UPCB). **Minas Gerais**: Descoberto, Reserva Biológica do Grama, trilha principal, 15 Jun 2005, *Jascone et al. 428* (RB) ; Rio Preto, RPPN Mato Limpo, Mata da Cachoeira, 06 Oct 2007, *Salimena 2503* (MBM). **Paraná**: Antonina, Reserva Natural Rio Cachoeira (SPVS), Trilha do Corvo, 25°19′00″S, 48°40′00″W, 100 m, 01 May 2005, *Matos et al. 554* (MBM, UPCB); Campina Grande do Sul, Parque Estadual Pico Paraná, Morro Camapuã, 25°15′00″S, 48°50′00″W, 1200-1300 m, 09 Apr 2009, *Pereira 475* (NY, UPCB); Curitiba, Parque Barigui, 25°25′35″S, 49°18′27″W, 18 Jun 1996, *Kozera 152* (MBM, UPCB); Guaraqueçaba, Morro do Quitumbê ou do Costão, 25°17′00″S, 48°20′00″W, 17 Jul 1994, *Athayde et al. 105* (MBM, UPCB); Guaratuba, Pedra Branca de Araraquara, 25 May 1947, *Hatschbach 716* (MBM, RB); Morretes, Estrada da Graciosa, Grota Funda, 25°20′25″S, 48°53′42″W, 19 Oct 1963, *Hatschbach 10750* (MBM, UPCB); Morretes, Parque Estadual do Marumbi, 25°27′13″S, 48°55′11″W, 800 m, 02 Sep 2006, *Labiak 3750* (UPCB); Paranaguá, Ilha do Mel, Morro Bento Alves, 25°32′07″S, 48°19′52″W, 28 Mar 1999, *Kozera 1009* (MBM, UPCB); Piraquara, Mananciais da Serra, encosta ocidental da Serra do Mar, 25°29′47″S, 48°58′51″W, 1050 m, 06 Jul 1998, *Dittrich 397* (MBM, UPCB); Ponta Grossa, Parque Estadual de Vila Velha, capão da Fortaleza, 25°14′17″S, 50°00′39″W, 21 Aug 2004, *Schwartsburd et al. 311* (UPCB); São José dos Pinhais, Usina Hidrelétrica de Guaricana, 02 Jun 1986, *Motta 270* (MBM); Telêmaco Borba, UHE Mauá, 21 Feb 2012, *Canestraro et al. 311* (MBM); Tibagi, Parque Estadual do Guartelá, 24°39′10″S, 50°15′25″W, 870 m, 21 Aug 2010, *Michelon 928* (UPCB); Tunas do Paraná, Parque Estadual de Campinhos, 08 May 1998, *Ribas et al. 2647* (MBM). **Rio de Janeiro**: Angra dos

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holoepiphytic plant. **F.** *C. crispum*, primary hemiepiphyte, removed from trunk to show the mass of long feeding roots (arrow) extending to the soil. **G, J.** *C. herbaceum*, rhizome with dark brown scales **H, K.** *C. atlanticum*, rhizome with orange-brown scales **I, L.** *C. crispum*, rhizome with orange-brown scales (Photos by F. Matos.)

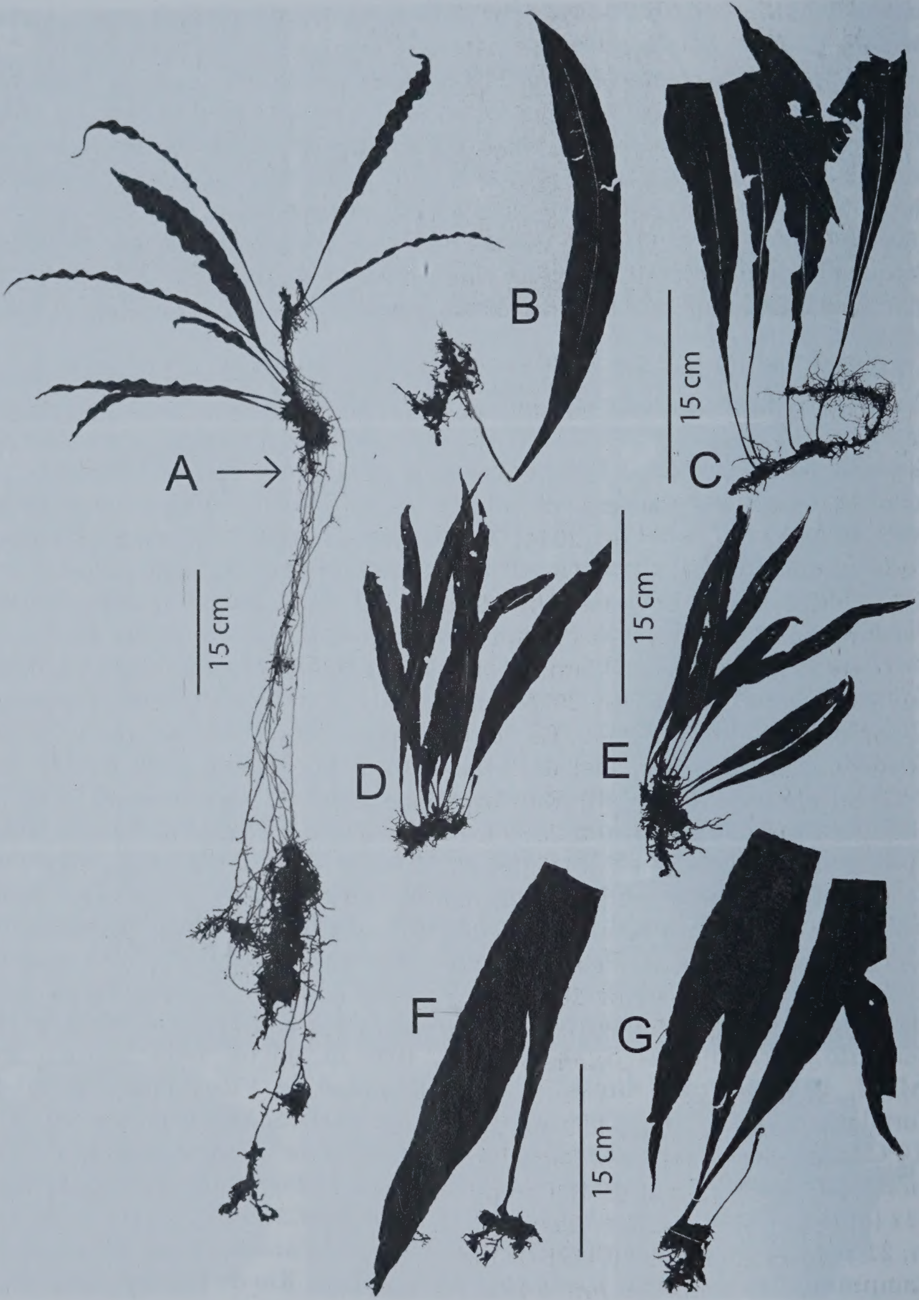

FIG. 2. Three closely related species of *Campyloneurum* endemic (or nearly so) to southeastern Brazil. **A.** Silhouette of *C. atlanticum* removed from trunk, showing leaves at top, climbing rhizome whose base is indicated by the arrow, and long feeding-roots that descend to the soil. (Modified from photo by F. Matos). **B–C.** Silhouette of *C. atlanticum*. **D–E.** Silhouette of *C. herbaceum*. **F–G.** Silhouette of *C. crispum*. (A from *Hirai et al. 673*, NY; D from *Labiak et al. 4364*, NY; E from *Braga 5780*, NY; F from *Jonsson 97*, NY; G from *Santos & Matos-Silva 3717*, NY.)

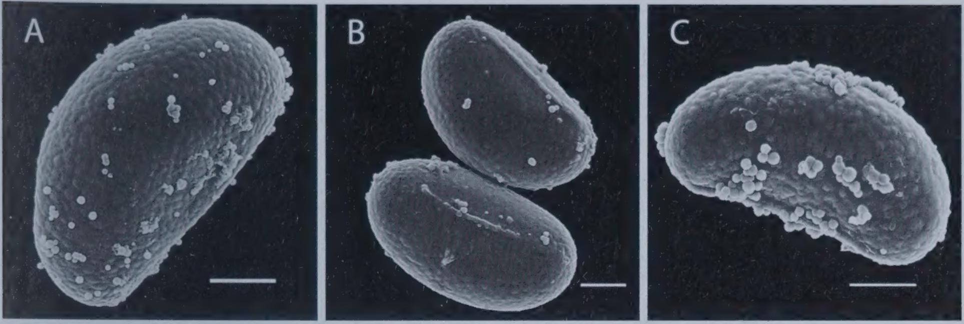

FIG. 3. Spores of three species of *Campyloneurum*. The small round spheres on the spores surfaces are fungal spores. **A.** *C. atlanticum*. **B.** *C. crispum*. **C.** *C. herbaceum*. Scale bars = 10 micrometers. (A from *Vanni et al. 781*, MO; B from *Thomas et al. 14230*, NY; C from *Mexia 4243*, NY.)

Reis, Mambucaba, Reserva da Electronuclear, trilha Porã, 22°59′51″S, 43°00′00″W, 150 m, 16 Jul 2014, *Mynssen 1426* (NY, RB); Itatiaia, Parque Nacional do Itatiaia, 22°27′04″S, 44°36′40″W, 800 m, 09 Feb 2013, *Labiak et al. 5470* (UPCB); Macaé de Cima, Alto Macaché, 12 Mar 1870, *Glaziou 4427* (NY); Mangaratiba, Reserva Rio das Pedras, trilha do Corisco, 600 m, 21 Jan 2000, *Mynssen 323* (RB); Paraty, Parque Nacional da Serra da Bocaina, 23°10′15″S, 44°50′08″W, 1450 m, 07 Jan 2008, *Labiak et al. 4357* (UPCB); Rio de Janeiro, Arboreto do Jardim Botânico, Canteiro 40 B, 12 May 2003, *Simões 38* (RB); Teresópolis, Parque Nacional da Serra dos Órgãos, plot 6, 1380 m, 24 Nov 2004, *Engelmann RE106* (RB). **Rio Grande do Sul**: Jaquirana, Fazenda Vitória, 900 m, 18 Mar 2005, *Wasum 2588* (MBM); Monte Belo do Sul, Linha Santa Bárbara - Saúde, 29°9′46″S, 51°37′55″W, 600 m, 7 Aug 2011, *Gonzatti 37361* (MO); Nova Petrópolis, 13 Jun 1949, *Rambo 41938* (RB); Santa Tereza , Linha Pederneira - Reserva Brum, 161 m, 07 Jan 2012, *Gonzatti 301* (FURB, RB). **Santa Catarina**: Bela Vista do Toldo, Serra do Lucindo, 26°16′36″S, 50°27′50″W, 866 m, 27 Nov 2007, *Gasper 1069* (UPCB); Benedito, Novo Alto São João, 690 m, 25 May 2010, *Dreveck 2223* (FURB); Blumenau, Faxinal do Bepe, Parque Nacional da Serra do Itajaí, 780 m, 25 Oct 2009, *Gasper 2454* (FURB); Bom Princípio, 101 m, 11 Jan 2008, *Gasper et al. 1209* (FURB); Braço do Salão, Fazenda Sabiá, 533 m, 27 Oct 2009, *Schmitt et al. 413* (FURB); Campo Belo do Sul, Fazenda Gateados, 27°59′24″S, 50°53′42″W, 875 m, 13 Dec 2008, *Verdi et al. 1209* (MBM); Campo Novo, acesso alternativo ao Campo dos Padres, 120 m, 12 Nov 2011, *Gasper et al. 2912* (FURB); Cubatão, 116 m, 06 Jul 2010, *Cadorin et al. 2900* (FURB); Florianópolis, Morro da Lagoa, 27°34′36″S, 48°28′32″W, 444 m, 19 Jun 2010, *Cadorin et al. 2645* (FURB, MBM); Forquilhinha, 666 m, 28 Jan 2010, *Schmitt et al. 1082* (FURB); Guarani, 335 m, 07 Mar 2011, *Korte 6158* (FURB); Ipira, Comunidade de Linha Capelinha, 27°24′11″S, 51°47′03″W, 29 Apr 2013, *Imig 150* (UPCB); Itajaí, Morro do Baú, ao longo da trilha para o topo, 750 m, 09 Apr 1994, *Falkenberg 6619* (FURB); Jaraguá do Sul, Rio Manso, 770 m, 29 May 2010, *Cadorin et al. 2535* (FURB);

Joinville, Condomínio Perini Business Park, 20 m, 03 Feb 2015, *Gasper 3658* (FURB); Meleiro, 28° 49′30″ S, 49° 38′18″ W, 01 Dec 1943, *Reitz C207* (RB); Ponte Alta, Morro do Funil, 27°29′03″S, 50°22′41″W, 1135 m, 25 Mar 2008, *Gasper 1648* (UPCB); São Bento do Sul, Arredores do Cepa Rugendas-Univille, Rio Natal, 26°15′02″S, 49°22′43″W, 28 Mar 2008, *Meyer 651* (UPCB); São Francisco do Sul, Estaleiro, trilha da captação, 25 Jul 2007, *Berger 777* (MBM); Vidal Ramos, Mulungu, 761 m, 14 Sep 2009, *Korte 80* (FURB, RB). **São Paulo**: Iguape, Reserva Ecológica de Juréia, trilha da margen do Río Verde, 24°42′29″S, 47°33′19″W, 15 Aug 1990, *Prado et al. 339* (NY); Jundiaí, Serra do Japi, 13°15′S, 46°56′W, 1116 m, 14 Nov 2009, *Hirai et al. 673* (NY); Matão, fragmento G-09, 21°37′S, 48°32′W, 400 m, 12 Dec 2007, *Prado et al. 1762* (NY); Paranapiacaba, Alto da Serra, 22°53′S, 44°14′W, Jun 1910, *Luederwaldt 22080* (NY); Campos do Jordão, 1600 m, Jun 1946, *Leite s.n.* (RB); Cananéia, Ilha do Cardoso, Morro Três Irmãos, 25°00′53″S, 47°55′36″W, 27 Sep 1989, *Barros 1745* (NY); Caraguatatuba, Reserva Forestal de Caraguatatuba, about 3 1/2 km NNW of Caraguatatuba, 23°50′46″S, 46°37′47″W, 20 May 1961, *Eiten 2840* (NY); Iporanga, Parque Estadual Turístico do Alto Ribeira (PETAR), Base Areado Iporanga, 06 Jul 2012, *Mazziero 1092* (RB); Peruíbe, caminho para Guara, 13 Jul 1969, *Windisch 25* (K); Rio Grande, 1906, *Wacket s.n.* (RB); São Paulo, Serra da Cantareira, 1000 m, Jun 1913, *Toledo Jr. s.n.* (RB); Serra da Bocaina, 1650 m, 16 May 1951, *Brade 20989* (MO, NY, RB).

PARAGUAY. Guaira: Cordillera de Ybytyruzú, road to Cantera Jhú, 15 km N of Antena, along Arroy Tacurara, 24°45′S, 56°20′W, *Zardini 14098* (MO); Cordillera de Ybytyruzú, road to Cantera Jhú, 8 km S of route to Coronel Oviedo, 25°48′S, 56°20′W, 27 Sep 1989, *Zardini 14678* (MO). **Paraguarí**: Parque Nacional Ybycui, Arroyo Guaraní cerca de la catarata, 26°01′00″S, 57°03′00″W, 200 m, 21 Dec 1980, *Abrell 32* (MO); Parque Nacional Ybycui, vecino al Salto Guaraní, 26°03′00″S, 56°50′00″W, 05 Jun 1989, *Aguayo 288* (MO).

Distribution.—Atlantic Rain Forest of southeastern and southern Brazil, with extensions into the western regions of Paraguay and Argentina (Fig. 4)

Campyloneurum atlanticum is characterized by long creeping rhizomes, ovate rhizome scales, spreading and light castaneous to nearly orange, petioles that are 3.5–10.0 cm long, and laminae that vary in width from 2.0–4.3 cm. Plants are usually holoepiphytic on the base of tree trunks but may become a primary hemiepiphyte (sensu Benzing, 2008) when they produce long roots that reach the soil. The specific epithet refers to the Atlantic rainforests of southeastern Brazil.

Campyloneurum crispum Fée, Mém. Foug. 5. Gen. Filic. 259. 1852. Type: Brazil. [State unknown], 1817–1820, *C.F.P. Martius 303* (lectotype, here designated: RB (barcode 00683117); isolectotype: BM [BM001019817]. (Fig. 1 D–F, I, and L, and Fig. 2 F–G)

Campyloneurum acrocarpon Fée, Crypt. Vasc. Brésil 1: 115, t. 35, f. 3. 1869. Type: Brazil. *A.F.M. Glaziou 2820* [published in error as "*2801*"] (holotype?: P, barcode P01336413).

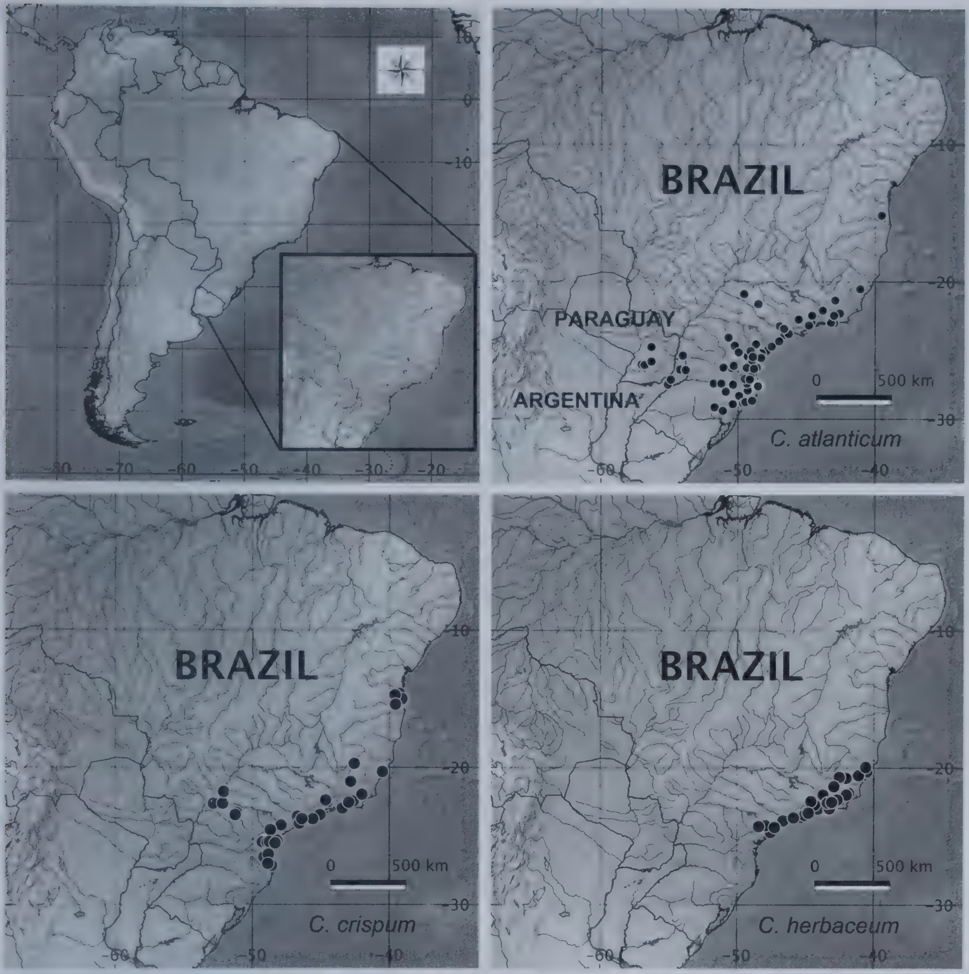

FIG. 4. Distribution maps for *Campyloneurum atlanticum, C. crispum*, and *C. herbaceum.*

Campyloneurum wacketii Lellinger, Amer. Fern J. 78: 27. 1988. TYPE: Brazil. **São Paulo**: Rio Grande, no date, *Wacket s.n.*[*Ros. Fil. Austrobras. Exs. 213*] (holotype US; isotypes GH, UC).

Plants terrestrial or epiphytic. Rhizomes short to long creeping, 3–5 mm wide; rhizome scales 1.0–1.5 mm long, ovate-lanceolate, slightly bullate, dark to orange brown, cells more or less isodiametric, irregular. Leaves 30–120 cm long; petioles 0.5–3.5 cm, ratio to leaf length 10–134; laminae 4.3–8.0 cm wide, lanceolate, long decurrent at the base, acuminate at the apex, chartaceous; sori in (7–)8–10(–12) rows between the costa and the margin.

Specimens examined.—**BRAZIL. Bahia**: Almadina, Serra do Corcovado, 9.8 km SW of Coaraci on road to Almadina, then N into Fazenda São José, 14°42′21″S, 39°36′12″W, 650-750 m, 29 Jan 2005, *Matos et al. 249* (NY, UPCB); Arataca, Serra das Lontras, ca. 7 km no ramal que liga o povoado de Itatinguí à Serra das Lontras, 15°23′30″S, 39°33′55″W, 600 m, 12 Feb 2005, *Matos et al. 424* (UPCB); Camacan, Fazenda Serra Bonita, 9,7 km W de Camacan na estrada para Jacarecí, daí 6 km SW na estrada para a RPPN e Torre da Embratel, 15°23′30″S, 39°33′55″W, 835 m, 03 Feb 2005, *Matos et al. 289* (UPCB); Ilhéus, 14.7 km west of Olivença on road to Vila Brasil, 14°58′55″S, 39°05′18″W 14 Feb 1994, *Thomas et al. 10385* (MBM, NY); Santa Luzia, Entrada a 11,3 km a E da sede do município "Serra da Onça", ca. 4,5 km entrada, 15°18′00″S, 39°19′00″W, 510 m, 23 Jul 1996, *Jardim et al. 848* (CEPEC, NY, UPCB); Una, BR 101 km 9 de São José a Una, 15°10′23″S, 39°07′56″W, 20 Jan 1982, *dos Santos 3717* (NY). **Espírito Santo**: Cariacica, Reserva Biológica Duas Bocas, Localidade de Alegre, trilha do Pau-Oco, 20°16′04″S, 40°31′30″W, 525 m, 22 Jul 2008, *Labiak et al. 4898* (CEPEC, MBML, RB, UPCB). **Espírito Santo**: Marlieria, Parque Estadual do Rio Doce, Campolina section, 19°42′23″S, 42°34′33" W, 25 Sep 1975, *Heringer 15226* (NY); Distrito Rio Branco, Retiro de Antonio Avelino, not found, 750 m, 13 Nov 1930, *Mexia 5298* (NY). **Paraná**: Antonina, Reserva Natural Rio Cachoeira (SPVS), Trilha da Guaricica, 25°15′00″S, 48°41′00″W, 30 m, 15 Jan 2005, *Matos 198* (MBM, UPCB); Curitiba, Parque Barigui, 25°25′35″S, 49°18′27″W, 22 Aug 1995, *Carrião et al. 26036* (NY); Diamante do Norte, Estação Ecológica de Caiuá, ribeirão Diamante, 22°37′06″S, 52°51′23″W, *Silva et al. 2531* (MBM); Guaraqueçaba, Morro do Rio das Pacas, 25°25′00″S, 48°15′00″W, 0–180 m, 20 Jan 1993, *Prado et al. 472* (MBM, UPCB); Guaratuba, Ilha do Barigui, Jul 1951, *Frenzel s.n.* (MBM); Jacareí, 26°31′17″S, 49°10′06″W, 20 Mar 1914, *Jonsson 97* (NY); Londrina, Bosque do IAPAR, 31 Aug 1976, *Dombrowski 3930* (MBM); Morretes, Parque Estadual do Marumbi, 25°27′13″S, 48°55′11″W, 200 m, 15 Oct 2004, *Labiak et al. 3374* (UPCB); Paranaguá, Estação Ecológica de Guaraguaçu, seguindo pela Rodovia Eng. Argus Thá Heyn (PR-407) no sentido para Pontal do Paraná, entrada a esquerda logo após a ponte sobre o Rio Guaraguaçu, 25°39′00″S, 48°29′48″W, 10 m, 25 Apr 2016, *Matos 2550* (UPCB); Pontal do Paraná, Ilha do Mel, 25°30′42″S, 48°20′20″W, 03-05 m, 28 Nov 1970, *Hatschbach 25680* (MBM). **Rio de Janeiro**: Cachoeiras de Macacu, Street between Funchal and Guapiaçu, near REGUA, 22°27′46″S, 42°39′10″W, 31 m, 18 Oct 2009, *Baber KB271* (MBM); Guapimirim, Estação Ecológica Estadual de Paraíso, Caminho para o Morro do Pirulito, Vale do Rio Falcão, 22°32′13″S, 42°58′55″W, 22 Nov 1991, *Sylvestre et al. 699* (RB); Itatiaia, Margem do rio Campo Belo, entre o Lago Azul e o rio Taquaral (abrigo lV), 22°22′31″S, 44°39′44″W 29 Sep 2005, *Sylvestre et al. 1809* (RB); Rio de Janeiro, Maciço da Pedra Branca, caminho para Represa do Camorim, 22°57′57″S, 43°26′20″W, 29 Sep 1980, *da Rocha 18339* (NY); Santa Maria Magdalena, , 21°57′19″S, 42°00′29″W 27 Jul 2012, *Labiak et al. 5392* (RB, SP, UPCB). **Santa Catarina**: Araquari, Ilha dos Barcos, 09 Mar 2001, *Ribas et al. 3408* (MBM); Brusque, Barracão, 27°00′20″S, 48°52′11″W, 45 m, 17 Nov 2009, *Stival-Santos et al. 1199* (FURB, MBM, RB); Itapoá, Reserva Volta Velha, 26°04′56″S, 48°38′26″W 25 Sep 1994, *Labiak 213*

(MBM, UPCB); Joinville, Pirabeiraba, 26°19′13″S, 48°50′37″W, Mar 1904, *Schmalz 13* (NY); Piçarras, Bela Vista, 26°43′48″S, 48°41′40″W, 10 Oct 2009, *Dreveck 1115* (MBM); Porto Belo, 27°08′58″S, 48°36′07″W, 55 m, 05 Feb 2010, *Schmitt et al. 1319* (MBM). **São Paulo:** Iporanga, Parque Estadual Turístico do Alto Ribeira (PETAR), Núcleo Santana, 24°32′22″S, 48°41′36″W, 21 Sep 2011, *Mazziero 592* (NY, UPCB); Praia Grande, Jardim Real, Estrada Mongaguá-Praia Grande Km 300 SP-64, 24°04′22″S, 46°35′01″W, 11 m, 25 Oct 2007, *Lobão et al. 1444* (UPCB); Presidente Epitácio, Margens do rio Paranapanema em área da Reserva Florestal do Morro do Diabo a ser inundada pela construção de barragem de usina hidrelétrica, 21°45′53″S, 52°06′19″W, Sep 1985, *Windisch 4247* (UPCB); São Sebastião, Parque Estadual da Serra do Mar, trilha das cachoeiras do Ribeirão Itú, 23°45′00″S, 45°36′00″W 20 Apr 2000, *Salino et al. 5328* (MBM); Sete Barras, Parque Estadual Carlos Botelho, núcleo de Sete Barras, 24°12′00″S, 47°55′00″W, 120 m, 27 Sep 2002, *Dittrich 1205* (MBM); Teodoro Sampaio, Região do Pontal do Paranapanema, Parque Estadual Morro do Diabo, ca. 17 km da cidade. Rodovia SP 613/Teodoro Sampaio-Rosana, ca. 5 km da Rodovia pela trilha, Córrego do Caldeirão, 22°32′00″S, 52°11′00″W, 350-450 m, 17 Jan 1995, *da Silva et al. 1624* (MBM); Ubatuba, Região Sul de Ubatuba, 23°26′22″S, 45°04′12″W, 140 m, 07 Sep 1998, *Dittrich 473* (MBM, UPCB).

Distribution.—Endemic to the Atlantic Rain Forest of Brazil, in the states of Bahia, Espírito Santo, Rio de Janeiro, Minas Gerais, São Paulo, Paraná, and Santa Catarina; wet forests, 0–835 m (Fig. 4).

Campyloneurum crispum resembles *C. atlanticum* and *C. herbaceum* by having similar rhizome scales, which are ovate and spreading. It differs, however, by its larger laminae (up to 120 cm long), and by its short and compact rhizomes (Fig. 2 F–G). It is commonly terrestrial or epiphytic. When epiphytic, the plants are usually growing on the base of tree trunks, and sometimes they also have feeding roots that reach the soil as seen in both *C. atlanticum* and *C. herbaceum.*

We chose the specimen at RB as the lectotype of *Campyloneurum crispum* because it has Fée's label and handwriting. The isolectotype at BM is the same species but lacks a label and Fée's handwriting. Martius collected in southeastern Brazil during the beginning of his trip (Urban, 1906). It seems likely that the lectotype was collected there.

The type collection (*Martius 303*) is mixed. We have excluded two of the syntypes with this number. The first is the sheet at P (barcode P01336248), which represents *Microgramma baldwinii* Brade, and the second is the sheet at MO, which appears to represent *Campyloneurum fuscosquamatum* Lellinger.

As to *Campyloneurum acrocarpon,* which is here placed in synonymy, it seems certain that the type number cited in the protologue, "*Glaziou 2801,*" is an error. That number applies to a species of *Blechnum.* Fee's illustration in the protologue matches well *Glaziou 2820.* It depicts a plant with two leaves (one leaf removed in the larger image, but the petiole clearly visible), and this matches *Glaziou 2820*, which also has two leaves. Although the laminae of the specimen are not folded as in the illustration, the upwardly curved tip of the rhizome and the sori restricted to the distal part of the lamina match well with the specimen.

Campyloneurum herbaceum (Christ in Schwacke) Ching, Sunyatsenia 5: 263. 1940. *Polypodium herbaceum* Christ in Schwacke, Pl. Nov. Mineir. 2: 22. 1900. Type: Brazil. **Rio de Janeiro**: Corcovado, Paineiras, Serra da Carioca, 8 Mar 1886, *A. Schwacke 5384* (lectotype, here designated: P, barcode P00624652; isolectotype: BM, barcode BM000937405). (Fig. 1 C, G, and J, and Fig. 2 D–E)

Plants hemiepiphytic. Rhizomes long creeping, 1.5–3.0 mm wide; rhizome scales 1.0–1.3 mm long, ovate-lanceolate, slightly bullate, dark-brown to orange-brown, cells more or less isodiametric, irregular. Leaves 17–37 cm long; petioles 0.5–3.0 cm long, ratio to leaf length 8.6–34.0; laminae 1.8–2.6 cm wide, linear lanceolate, long acuminate at the base, acuminate at the apex, chartaceous; sori in (3)4–5 rows between the costa and the margin.

Specimens examined.—**BRAZIL. Espírito Santo**: Cariacica, Reserva Biológica Duas Bocas, Localidade de Alegre, trilha do Pau Oco, 20°16′00″S, 40°31′00″W, 590 m, 04 May 2008, *Fontana et al. 5136* (UPCB); Castelo, Parque Estadual do Forno Grande, Trilha da Balança, 20°31′37″S, 41°06′06″W, 1250-1600 m, 18 Jul 2008, *Labiak et al. 4830* (RB, UPCB); Santa Teresa, estrada em direção ao centro de Santa Teresa, mata adjacente com acesso pela casa n° 5, 19°56′09″S, 40°36′00″W, 24 Aug 2004, *Mynssen et al. 647* (NY, RB). **Minas Gerais**: Araponga, Fazenda da Serra, 20°40′1″S, 42°31′15″W, 3 Apr 1930, *Mexia 4656* (MO, NY); Carangola, Subida da serra da Grama, 20°43′58″S, 42°01′44″W, 19 Apr 1932, *Kuhlmann 124* (RB); Descoberto, Reserva Biológica da Represa do Grama, 21°20′50″S, 42°55′20″W, 10 Nov 2001, *Augustin et al. s.n.* (RB); Santa Bárbara do Monte Verde, Serra Negra - Fazenda Três Cruzes - Chapadão, 21°57′32″S, 43°42′07″W, 1200 m, 21 Apr 2004, *Condack 101* (RB). **Rio de Janeiro**: Angra dos Reis, Reserva da Usina Eletronuclear, 23°00′25″S, 44°19′04″W, 22 Mar 2003, *Mynssen 417* (RB); Guapimirim, Estação Ecológica Estadual de Paraíso Margem esquerda do rio Paraíso, em bifurcação, 22°26′00″S, 45°50′00″W, 150 m, 06 Dec 1984, *Pessoa et al. 9* (RB); Itatiaia, Parque Nacional do Itatiaia, 22°22′31″S, 44°39′44″W, 17 Jul 1902, *Dusén 693* (NY); Magé, Serra da Estrela, trilha entre Piabetá e Petrópolis, 22°34′09″S, 43°10′58″W, 500 m, 22 Feb 2010, *Engelmann RE0549* (RB); Mangaratiba, Reserva Biológica de Rio das Pedras, trilha para o Corisco, 22°59′00″S, 44°05′00″W, 550 m, 21 Jan 2000, *Santos et al. 1376* (RB); Miguel Pereira, Reserva Biológica do Tinguá Orbel 2 Trilha com acesso pelo km 31 Margens do Rio São Pedro, lado esquerdo do rio Miguel Pereira, 22°32′43″S, 43°23′05″W, 789 m, 11 Jul 2007, *Sylvestre et al. 2068* (RB); Nova Friburgo, Área da pousada Vale dos Sonhos, 22°22′10″S, 42°33′22″W, 1200 m, 01 May 2012, *Bonnet 88a* (UPCB); Paraty, APA Cairuçu. Morro do Corisco, 23°16′54″S, 44°47′05″W, 450 m, 03 Feb 2012, *Matos 2035* (MO, NY, RB, UPCB); Rio de Janeiro, Parque Nacional da Tijuca, Mata do Pai Ricardo, 22°57′47″S, 43°14′40″W, 500 m, 10 Jun 1976, *Carauta 2071* (RB); Santa Maria Madalena, Parque Estadual do

Desengano, Poço Parado, 21°49′58″S, 41°49′55″W, 961 m, 30 Mar 2011, *Mynssen et al. 1237* (MBM, NY, RB); Teresópolis, Flora da Serra dos Órgãos, picado do Rancho Frio, 22°26′43″S, 42°59′59″W, 1300 m, 20 Aug 1940, *Brade 16597* (MO, NY, RB). **São Paulo**: Cunha, Parque Estadual da Serra do Mar, núcleo Cunha-Indaiá, trilha do Río Bonito, 23°14′12" S, 45°01′15″W, 22 Jun 2006, *Henrique et al. 676* (NY); Paranapiacaba, Alto de Serra, 24°42′00″S, 47°33′00″W, 14 Aug 1912, *Brade 5236* (NY); Bananal, Nova Suiça, Sítio da Cachoeira, 22°41′02″S, 44°19′25″W, 26 Sep 1978, *Silva 121* (MBM); Iporanga, Fazenda Intervales, Trilha para o Mirante, 24°16′06″S, 48°24′50″W, 23 May 1996, *Prado et al. 953* (UPCB); Salesópolis, Estação Experimental de Boracéia, Picada da cachoeira do Pilão, 23°37′51″S, 45°52′11″W, 05 Mar 1962, *Travassos 372* (RB); Sete Barras, Parque Estadual Carlos Botelho, Núcleo Sete Barras, 24°12′00″S, 47°55′00″W, 300 m, 26 Sep 2002, *Dittrich 1187* (MBM); Ubatuba, Morro Corcovado, 23°26′22″S, 45°04′12″W, 08 Sep 1998, *Ribas 2716* (MBM).

Distribution.—Endemic to the Atlantic Rain Forest of Brazil, in the states of Espírito Santo, Rio de Janeiro, Minas Gerais and São Paulo; wet forests, 150–1600 m (Fig. 4).

The lectotype at P represents the species in question. It agrees in rhizome width, type of rhizome scales (ovate, dark castaneous, spreading), and narrower leaves. It may be distinguished from *C. atlanticum* by its smaller size and narrower laminae (1.8–2.6 cm), petioles up to 3 cm long, and darker rhizome scales (Fig. 1, G and J). In *C. atlanticum* the rhizome scales are light brown to nearly orange (Fig. 1, H and K), the laminae wider (2–4.3 cm), and the petioles longer (3.5–10.0 cm).

Names of Uncertain Application.—Our analysis on the types of *Campyloneurum lapathifolium* and *C. minus* revealed that they do not apply to the specimens from the Atlantic Rain Forest of Brazil, as follows:

Campyloneurum lapathifolium (Poir.) Ching, Sunyatsenia 5(4): 263. 1940. *Polypodium lapathifolium* Poir., Encycl. 5: 514. 1804. TYPE: Country unknown. "America meridionale," no date or collector (holotype: P-herb. Jussieu 1071-E, barcode P00674282; photo of P at BM, S).

The rhizome scales of *Campyloneurum lapathifolium* are dark brown and narrowly lanceolate. Although the type locality is not clearly stated on the label, we believe it was collected in the northern part of South America. The name probably applies to *C. fuscosquamatum* or *C. repens* (Aubl.) C. Presl.

Campyloneurum minus Fée, Mem. Foug., 5. Gen. Filic. 258. 1852. TYPE: "Habitat in America australi," no date or collector cited. Type: not found.

Fée published this name in 1852, mentioning that this species was probably from French Guyana. Later, in 1869, Fée placed it as a synonym of *C. fasciale* (Humb. & Bonpl. ex Willd.) C. Presl, a species from northern South America. We were unable to find the original material of *C. minus* at P, where most of Fée's types are housed. Searches at STR, where most of Fée's fern collections had been kept at first, and searches at NTM where some Fée's collections are still kept (Maddi et al. 2013), also failed to find a type.

Windisch (1982) cited *Glaziou s.n.* at RB (barcode 00682314) as a type of *Campyloneurum minus*, and an image of this specimen on JSTOR Global Images is annotated as "isotype." The Glaziou specimen, collected in Southeastern Brazil, does indeed represent the primary hemiepiphytic fern with which we are concerned in this paper. Glaziou, however, arrived in Brazil in 1858 (Urban, 1906), after the name was published, and therefore his specimen cannot be the type.

Although it remains unknown which is the precise type locality of *C. minus*, it seems clear that it is not from Southeastern Brazil. Furthermore, the comments provided by Fée, as well as the history of the botanical expeditions by Glaziou in Southeastern Brazil, strongly suggest that this name does not apply to the specimens from the Atlantic Rain Forest.

Because the type of *C. minus* cannot be found, we consider this name as a *nomen dubium.*

Growth habit.—We found that both *Campyloneurum atlanticum* and *C. herbaceum* were primary hemiepiphytes sensu Benzing (2008). Their gametophytes grow as epiphytes on the bases of trunks. Accordingly, all sporelings were located on the bases of trunks; none were found on the soil. Early in development, the sporelings send a single long and unbranched (rarely sparsely branched) root to the ground, where it branches profusely in the soil (Figs. 1 A–C, and 2 A). After this contact with the soil, the rhizome of the sporeling begins to climb, producing successively larger leaves (Fig. 2 A). Thus, the plants are not terrestrial root climbers sensu Darwin (1865); that is, plants that start on the soil and subsequently climb a trunk, maintaining contact with the soil throughout their lives.

This is the first report of the primary hemiepiphytic growth habit in *Campyloneurum.* No other species of *Campyloneurum* in southeastern Brazil has this growth habit (Labiak, pers. obs.). As might be expected given this shared growth habit, *C. atlanticum* and *C. herbaceum* are sister species (unpublished molecular phylogenetic data, Labiak and Moran). Elsewhere in the Polypodiaceae, primary hemiepiphytism has been described for *Colysis ampla* (F. Muell. ex Benth.) Copel. (Sundue and Testo, 2014) and *Pleopeltis bradeorum* (Rosenst.) A. R. Sm. and Tejero (Fawcett and Sundue, 2016). Among other Neotropical ferns, primary hemiepiphytism has been described in the Dryopteridaceae for *Elaphoglossum amygdalifolium* (Mett. ex Kuhn) Christ (Lagomarsino et al., 2012), and in the Hymenophyllaceae for *Vandenboschia collariata* (Bosch) Ebihara and K. Iwats. (Nita and Epps, 2009). The present study yields another example of this growth habit, which until recently had been overlooked in ferns.

Campyloneurum crispum has been reported as being terrestrial or, more rarely, epiphytic. When terrestrial, it grows on humus-rich soils. When epiphytic, it is generally restricted to the base of tree trunks. In some epiphytic specimens there are long roots that also grow towards the soil, resembling the feeding roots of *C. atlanticum* and *C. herbaceum*. However, whether this species is a facultative hemiepiphytic (i.e., the gametophytes were first established on the soil or on the base of the trunks) still remains to be determined.

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Appendix 1: List of Exsiccate

The number in parentheses refers to the species as follows: 1 = *Campyloneurum atlanticum*; 2 = *C. crispum*; 3 = *C. herbaceum.* Collection numbers in boldface indicate types.

Abrell, D.B. 32 (1)
Aguayo, A. 288 (1)
Alston, A.H.G. & Brade 8993 (3)
Amorim, A.M. et al. 4459 (2)
Ariati, V. et al. 1019 (1)
Athayde, S.F. et al. 105 (1), 303 (1)
Augustin, J.O. et al. s.n. (3)
Baber, K. & Wesenberg, J. KB174 (2), KB271 (2)
Barbosa, E. & Marinero, F. 1405 (1)
Berger, J.Z. 777 (1)
Bittencourt, F. et al. 38 (1), 46 (1)
Bonnet, A. & Caglioni, E. 88a (3), 88b (3)
Botelho, P. 16 (3)
Brade, A.C. 5236 (3), 9568 (3), 9795 (1), 16597 (3), 20989 (1)
Braga, J.M.A. 5780 (3)
Britez, R.M. 1131 (2)
Cabral, E.L. et al. 707 (1)
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Effects of Shade on Individual Ramet Growth and on Clonal Growth of the Aquatic Fern *Salvinia auriculata* (Salviniaceae)

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Abstract.—Light intensity is among the major environmental factors determining the ecological distribution of any plant. The effects of light availability on aquatic plants continue to be discussed, as some species show higher growth under full sun conditions and other species show reduced growth. The aim of this study was to test the effects of different shade levels on ramets and clonal growth of the fern *Salvinia auriculata*. We hypothesized that the ramets grow better under shade conditions over time as in most land ferns. We performed a greenhouse experiment, putting plants under three treatments: control (0% shade), 30% shade, and 70% shade. We monitored the growth of individual ramets as well as clonal spread for 30 days. The number of new ramets (clonal growth) increased exponentially in the three treatments, however this number was higher in shade than in full sun plots. The size of floating leaves, submerged leaves, and rhizomes was higher under shade treatments compared to individuals under sun treatment. Our results showed that *S. auriculata* has a high growth performance under shade environments, including both clonal growth and the size of individual ramets, similar to most land ferns. This species appears highly plastic as it also thrives under bright sun, which appears to be a consistent pattern among fern species in both terrestrial and aquatic environments. Because shade has been proposed as a treatment to control and manage aquatic plants, application of this treatment should be carefully considered depending of the species, especially when it involves aquatic fern species.

Key Words.—Light, greenhouse, macrophytes, management, plasticity, shading net

Aquatic plants are important indicator species of ecological status in aquatic ecosystems, but they can also cause harm especially when growth becomes uncontrolled (Julien, Center, and Tipping, 2002; Lorenzi, 2000). These plants can exhibit rapid growth rates and can influence aquatic environments, local economies, and human health (Jampeetong and Brix, 2009; Marcondes, Mustafá, and Tanaka, 2003). Among the species of aquatic plants, ferns in the genus *Salvinia* (Salviniaceae) are a potentially serious aquatic weed due its clonal growth that can result in rapid expansion on the water surface (Coelho, Lopes, and Sperber, 2005). Species of *Salvinia* may form thick mats covering more than 100 km^2 in just three months - choking lakes and waterways and reducing populations of other aquatic plants and animals (Oliver, 1993). These ferns can reproduce exponentially by vegetative fragments, with a leaf doubling time of 3.5 days (Nichols, Couch, and Al-Hamdani, 2000). *Salvinia auriculata* Aublet has been recognized as an invasive weed and an ecological problem in many regions around the world (Room 1983, 1988, 1990).

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Once these plants become invasive, it is essential to understand how they perform under a variety of abiotic conditions. Important factors affecting aquatic plants include light, depth, latitude, temperature, and water levels. Among these factors, light, and in particular light intensity, is a very important parameter because it influences photosynthesis and determines the ecological distribution of plants (Hudon, Lalonde, and Gagnon, 2000; Larcher, 2003; Poorter, 2001; Valladares and Niinemets, 2008; Zhu *et al.*, 2014).

The effects of light availability on aquatic plants are of significant interest. Macrophytes that live in full sun maximize light input and allocate resources by increasing aboveground biomass, especially increasing leaf area and length (Strand and Weisner, 2001; Vretare *et al.*, 2001). Studies have shown that this may enhance their photosynthetic area and increase growth (Garbey, Thiébaut, and Muller, 2006). Other macrophyte species, such as the aquatic fern *Marsilea villosa* Kaulf. grow best in moderate shade (Chau and Reyes, 2014). Indeed, most pteridophytes grow best in shaded environments (Huang *et al.*, 2011), but the shade tolerance is species specific and depends on phase of life (Riaño and Briones, 2015).

According to Sessa and Givnish (2014), light availability is the most important variable driving morphological and physiological adaptation in land ferns. However, the prevalence of this pattern in aquatic ferns is unknown. Due to rapid dispersal rate, serious invasive potential, and limited information on the impacts of light availability on aquatic ferns, the aim of this study was to test the effects of different shade levels on growth of *S. auriculata*. Based on the premise that light is an important variable driving morphological and physiological adaptation in ferns, it was hypothesized that the ramets grow better under shade conditions over time, and that full sun may reduce ramet growth.

MATERIALS AND METHODS

Studied species.—Salvinia auriculata is a free-floating fern found in diverse habitats, such as rivers, reservoirs, and lakes, capable of growing and developing very well in hot and sunny locations as in tropical regions (Lorenzi, 2000). The plant consists of ramets connected by rhizomes, which allows for the formation of broad colonies on the water surface. Each ramet consists of a node with two floating green leaves and one submerged leaf that functions as a root (Sculthorpe, 1967). The clone consists of genetically identical ramets that grow through asexual reproduction and remain connected, retaining integration between the parental ramet and its new ramets (Charpentier, Mesléard, and Thompson, 1998).

The submerged leaf produces sori surrounded by a globose indusium, called the sporocarp (De la Sota, 1962). The sporocarps are resistant structures and their production occurs during the dry period, when clonal growth is unfavorable. During flood periods, asexual reproduction is favored by formation of buds. Both sexual and asexual reproductive strategies allow the species to survive in places with seasonal inundation patterns, like temporary ponds that are subject to drought and flood periods (Coelho, Lopes, and Sperber, 2005).

Plants and experimental design.—Ramets of *Salvinia auriculata* were collected in a marginal pond that is influenced by the Rio Grande (21° 11′ 15″ S; 45° 05′ 02″ W), Minas Gerais, Brazil. In the greenhouse, the plants were washed to remove the organic matter and soil particles. Efforts were made to select ramets of the same size and appearance for the experiment.

From the selected plants, one ramet was placed in a 1L translucent plastic pot. The pots contained 8 cm of Hoagland-Arnon solution (Hoagland and Arnon, 1950) prepared in distilled water. The solution was exchanged once per week in order to clean the pot and to avoid algal proliferation. We tested the growth of individual ramets as well as clonal growth using three levels of shade: control (under 100% of natural light in the greenhouse), 35% shade, and 70% shade for a period of 30 days. To create the shade treatments we used two different manufactured shading nets (35% and 70% shade) over the pots. We used 15 pots per treatment, totaling 45 pots (N=45).

The experiment was run for a period of 30 days, and every tenth day all the ramets in the 45 pots were counted and measured. The initial time of the experiment was considered time 0 (T0), 10 days after T0 (T1), 20 days after T0 (T2) and the last evaluation after 30 days (T3). We measured the: 1) number of new ramets (clonal growth), 2) length and width of floating leaves, 3) length and diameter of submerged leaf, 4) and length of rhizome. These measurements can provide information about the growth of each plant component, such as leaf expansion (floating and submerged leaves) and rhizome expansion, which are responsible for the formation of the whole clone, and the expansion of *S. auriculata* on the water surface. Clonal growth was recorded as the number of new offshoots (ramets) produced.

Statistical analyses.—The data were normally distributed according to the Kolmogorov-Smirnov test. To evaluate the treatment effect and temporal variation of 1) the number of new ramets; 2) length and width of floating leaves; 3) length and diameter of submerged leaf; 4) and rhizome length during the study, we fitted a linear-mixed effects model. We specified random intercepts per individual to account for the temporal pseudo replication in our design. In the model, we considered treatment as a fixed factor with three levels (control, 35% shade, and 70% shade); time was also considered as a fixed factor and corresponded to days that we measured the variables in the greenhouse (T0, T1, T2, and T3). In the linear-mixed effect models, we

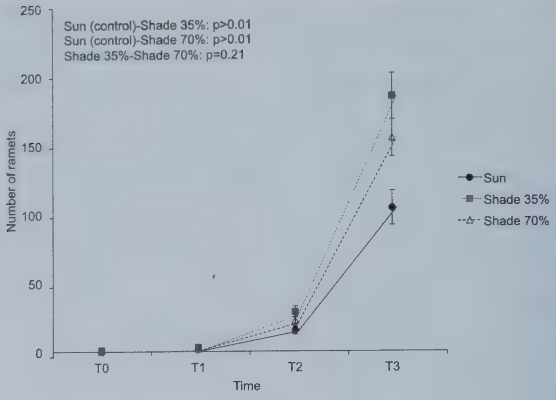

FIG. 1. Clonal growth of *Salvinia auriculata* under different shade treatments. The number of ramets measured during the experiment in sun (control), 35% shade, and 70% shade in T0, T1 (10 days after begin the experiment), T2 (20 days) and T3 (30 days). Data indicate significant differences among treatments at T3.

investigated differences between fixed factor levels (shade and time treatments) using 95% confidence intervals estimated by the model. The analyses were performed in R software.

RESULTS

Intact clones consisting of various sized ramets grew and filled the water surface in all the pots. The number of new ramets (clonal growth) increased exponentially in the three treatments (Fig. 1), however the number of ramets was higher in both shade treatments ($p<0.05$) than in the control pots (0% shade). The treatments alone did not have a significant effect on the number of ramets ($F=0.41$; $p=0.66$). The number of new ramets increased with time ($F=861.50$; $p=0.001$) and the interaction between treatments and time had a significant effect on the number of ramets. Clonal growth at T3 was lower in the control treatment and higher in the 35% and 70% shade (Fig. 1).

Considering the growth of individual ramets, the treatment alone did not have an effect on the variables, but time had a significant effect; there was an increase in all measurements (Table 1). The interaction between treatment and time also had a significant effect in the measured variables (Table 1). The length and width of floating leaves (Fig. 2a, b), length and diameter of submerged leaf (Fig. 2c, d), and length of the rhizome (Fig. 2e), in T2 and T3, were lower in control treatment (full sun) and higher in 35% and 70% shade.

DISCUSSION

Shade promoted an increase of individual ramet growth as well as clonal growth in the aquatic fern *Salvinia auriculata*, supporting our hypothesis. Under different levels of shade (35% and 70%), the plants produced longer

TABLE 1. Linear Mixed Model for the variables measured in the three treatments (control; 35% shade; 70% shade) at four different times (T0 – equal conditions for all treatments, T1, T2 and T3).

	Treatment		Time		Treatment x Time	
Ramets measures (cm)	*F*	*p*	*F*	*p*	*F*	*p*
Length of floating leaves	0.68	0.50	949.83	<0.001	3.47	0.03
Width of floating leaves	0.71	0.49	746.88	<0.001	3.32	0.03
Length of submerged leaf	0.26	0.77	718.94	<0.001	3.18	0.04
Diameter of submerged leaf	1.74	0.17	688.52	<0.001	2.71	0.07
Rhizome length	1.83	0.16	788.44	<0.001	3.51	0.03

rhizomes, larger floating leaves and submerged leaves, and a higher number of new ramets (offshoots). The same pattern was observed in *Marsilea villosa*, an endemic Hawaiian fern, which grows more vigorously under shade than under sun, especially in moderate shade (Chau and Reyes, 2014), just as we observed in *S. auriculata*.

Rapid growth is a feature of the life strategy of *Salvinia auriculata*. Species with such a strategy quickly and effectively occupy free space (Seastedt, 2009). For example, according to Galka and Szmeja (2013), the number of modules in a *S. natans* clone increased at the rate of 0.6/day, initiating a new module every second day on average. In our experiment, the colonies of *S. auriculata* grew from a single ramet and covered the surface of the pots in just 30 days. In addition, *S. auriculata* showed increased clonal growth under 35% shade, but the new ramets also grew under the other treatments. Clone formation undoubtedly is one of the features facilitating the expansion of *S. natans, S. molesta* (Room, 1983), and *S. auriculata* (Coelho, Lopes, and Sperber, 2005), especially under shade conditions, as we observed. Asexual modes are usually induced by adverse environmental conditions or by a lack of resource availability, inhibiting the normal life cycle (Barrett, Eckert, and Husband., 1993). Clonal growth may enable to the plant to maximize the leaf photosynthetic area, due to the numeric increase in physiologically independent plant units (ramets) by clonal means. The production of new ramets improves occupation and exploration of the environment. In addition, it increases the probability that the genet will survive (Cook, 1979). In this way, shade does not limit clonal growth of *S. auriculata*, on the contrary, it produces more new ramets.

Our study shows that all measures of the individual ramet growth (length of floating and submerged leaves, length of rhizome and diameter of submerged leaf) were higher in moderate shade (35%) at the end of the experiment (T3) (Fig. 2; Table 1). Thouvenot, Haury, and Thiébaut (2013) observed in the aquatic plant *Ludwigia grandiflora* (Onagraceae) that stem lengths and leaf areas were stimulated under reduced light (70% of sunlight intensity) and were greater in the shade than in full sunlight. Zutshi and Vass (1971) also reported considerable increase in the fresh weight of plants of *S. natans* under partial shade in laboratory conditions. Macrophytes increase leaf area and stem length in order to capture more light in the aquatic environment and to

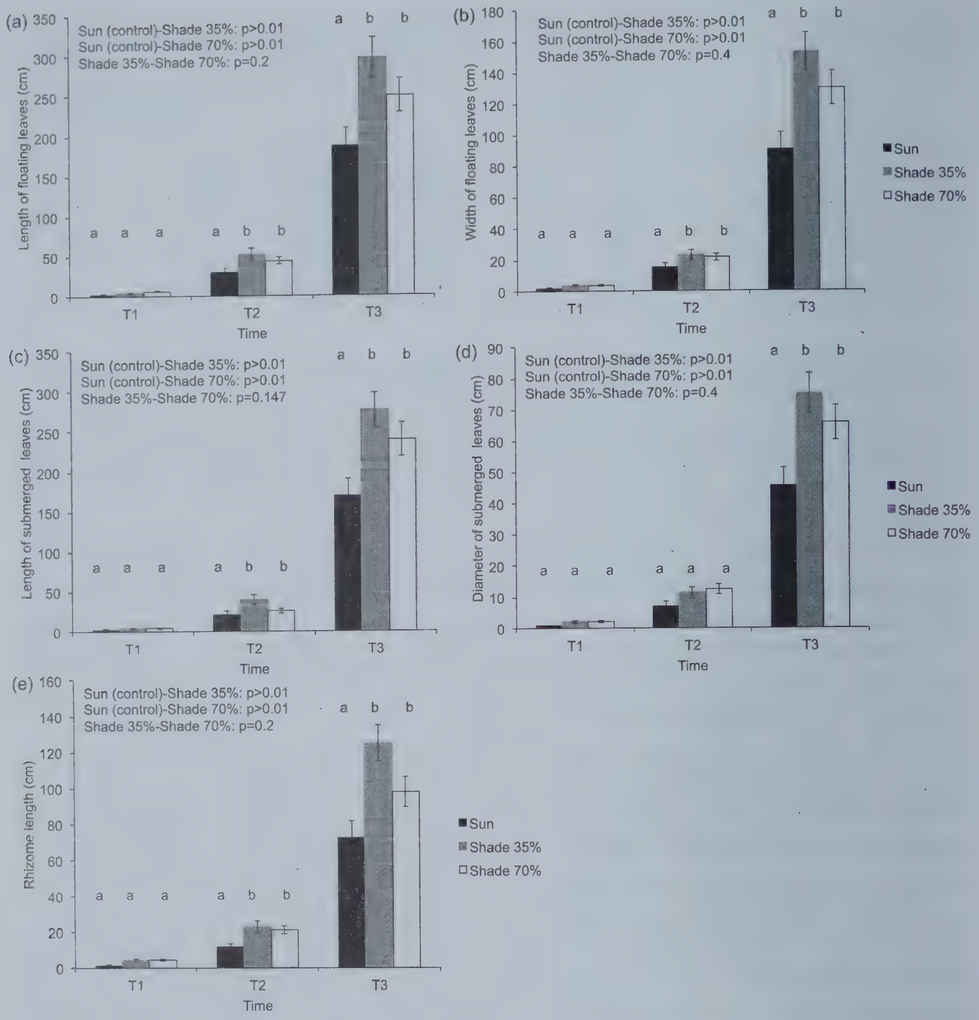

FIG. 2. The growth of individual ramets in *Salvinia auriculata*. Variables measured during the experiment in sun (control), 35% shade, and 70% shade in T1 (10 days after initiating the experiment), T2 (20 days), and T3 (30 days). (A) Length of floating leaves (cm); (B) Width of floating leaves (cm); (C) Length of submerged leaves (cm); (D) Diameter of submerged leaves (cm); (E) Rhizome length (cm). Different letters in each time indicate significant differences between treatments ($p>0.05$).

optimize photosynthesis (Garbey, Thiébaut, and Muller, 2006). The higher growth of *S. auriculata* under shaded conditions could be a compensatory mechanism to acquire more light and maintain physiological function.

Over the duration of the experiment, we observed changes in how the different treatments influenced both individual and clonal growth. At the beginning of ramet development, all structures of the plant grew similarly in both sun and shade. However, starting at T2 (20 days), whereas we observed enhanced growth of the ramets and their structures in the shade, the full sun treatment began to be detrimental for plant development. Although *S. auriculata* can be found in environments with high incidence of sun, shade environments could be the ideal conditions for this species development, as has been observed in other fern species (Chau and Reyes, 2014).

Due to rapid growth, *Salvinia* can form a "mat" that covers large portions of the water body where it grows (Gaudet, 1973; Nichols, Couch, and Al-Hamdani, 2000; Room, 1990). Because *S. auriculata* can be an invasive weed, control measures of this species (*e.g.* mechanical removal, biological and chemical control) have been studied. Recently, Zhu *et al.* (2014) tested the effect of shade on growth in the invasive macrophyte *Hydrocharis morsus-ranae* (Hydrocharitaceae) and they reported that 70 and 100% shade was effective at reducing biomass and controlling this species. Thus, in some cases shading may be considered by aquatic plant managers as one of the possible control methods (Zhu *et al.*, 2014). Our findings indicate that 70% shade does not prevent individual ramet growth or clonal growth of *S. auriculata*. Indeed, the species grows better in moderate and intense shade (35% and 70%) than in full sun.

To propose management tools for control of invasive and weedy species, it is important to know their response to a variety of environmental conditions and resources. In our study, *S. auriculata* responded differently than *Hydrocharis morsus-ranae* did in the Zhu *et al.* (2014) study. *Salvinia auriculata* grows better under shade environments, a pattern reported in some fern species from both terrestrial and aquatic environments (Chau and Reyes, 2014; Huang *et al.*, 2011; Zutshi and Vass, 1971). It is evident that this plasticity in the growth of individual ramets and the vigorous numerical increase of offshoots in the clonal growth contribute to the ability of *S. auriculata* to thrive in a wide range of habitats and explain its weedy behavior in some regions. Given that shade has been proposed to control and manage aquatic plants, our study indicates that it may not be recommended in all species, especially when it involves aquatic ferns.

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The Comparative Anatomy of *Hymenophyllopsis* and *Cyathea* (Cyatheaceae): a Striking Case of Heterochrony in Fern Evolution

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Abstract.—After a long history of taxonomic isolation, recent studies show that *Hymenophyllopsis* K.I.Goebel is nested within the tree fern genus *Cyathea* Sm. *s.s.*. We compare developmental stages of typical *Cyathea* with an anatomical survey of *Hymenophyllopsis*. Such comparisons should clarify how the distinctive features of *Hymenophyllopsis* are related to or derived from those of typical *Cyathea*. *Hymenophyllopsis* and *Cyathea* samples from field-preserved materials and herbarium specimens were examined using standard light microscopy techniques. *Hymenophyllopsis* species have simple stem anatomy: all have solenosteles or simple dictyosteles, and sclerenchyma and secretory strands are lacking. Only *H. superba* has as many as four vascular bundles in the petiole base. Leaf blades lack stomata, the epidermal cells contain chloroplasts and there are only one or two mesophyll layers. Typical adult *Cyathea* species have complex stelar anatomy with medullary bundles (some with cortical bundles) and complex stem histology. There are numerous vascular bundles in the petiole. Leaf epidermal cells other than guard cells lack chloroplasts and the mesophyll has multiple layers. In contrast to their differences from adult *Cyathea* plants, *Hymenophyllopsis* anatomy corresponds closely to early stages of young *Cyathea* sporophyte development. The origin of "*Hymenophyllopsis*" from typical *Cyathea* ancestors involved a drastic reduction in size and anatomical complexity, with the precocious production of spores. This is a clear example of paedomorphosis among pteridophytes, where *Hymenophyllopsis* adult plants represent precociously fertile, permanent "young sporophytes" of tree ferns.

Key Words.—evolutionary reduction, neoteny, paedomorphosis

Hymenophyllopsis K.I.Goebel until recently was understood to be a distinctive genus of eight named species of small filmy-leaved ferns, endemic to the tepuis of the Guyana Highlands of Venezuela and adjacent countries. The genus was placed in its own family, the Hymenophyllopsidaceae Pic.Serm., which was generally seen as a problematic group having no clear affinities with other fern families. Today, the taxonomy and affinities of *Hymenophyllopsis* within the ferns has been greatly clarified based on molecular studies. A study of *rbcL* sequences (Wolf *et al.*, 1999) found *Hymenophyllopsis* to belong to the tree fern clade, where the two species tested were sister to the single representative of typical Cyatheaceae that was included in their analysis. Subsequent studies including many more species of scaly tree ferns (e.g., Korall *et al.*, 2006, 2007; Janssen *et al.*, 2008; Bystriakova *et al.*, 2011; Korall & Pryer, 2014) have consistently shown that not only are

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Hymenophyllopsis species members of the scaly tree fern family Cyatheaceae, they are in fact embedded within the genus *Cyathea* Sm. *sensu stricto*.

The conclusion that *Hymenophyllopsis* is correctly placed in the genus *Cyathea* follows a history of many years of uncertainty concerning the relationship of the "family Hymenophyllopsidaceae" to other ferns. The genus *Hymenophyllopsis* was first described by Goebel in 1929, when he showed that the single species known to him was clearly distinct from *Hymenophyllum* (Hymenophyllaceae)—a large genus of filmy ferns with which the first species discovered was previously confused. Goebel (1929) gave a detailed description of morphological and anatomical characters to establish the new genus and species: *Hymenophyllopsis dejecta* K.I.Goebel. In his description and discussion he noted that given its particular combination of characters the species could represent a new family. He did not, however, formally name the family. It is noteworthy that he described some characters that led him to suggest a possible relationship with Cyatheaceae, which seems prescient in view of the recent classification of the group.

Although it has long been the taxonomic consensus that *Hymenophyllopsis dejecta* K.I.Goebel represented the same species as the earlier *Hymenophyllum dejectum* Baker, a more careful study of Goebel's descriptions and figures makes it clear to us that his new species in fact corresponds instead to the separate species described much later as *Hymenophyllopsis ctenitoides* Lellinger.

Goebel described *Hymenophyllopsis* as having stems with a simple solenostelic vascular system. In contrast, typical Cyatheaceae have long been known for their extremely complex histology and vascular anatomy, including complex systems of medullary and cortical vascular bundles (e.g., Adams, 1977; Kao, *et al.*, 2015; Lucansky, 1974, 1976a, 1977, 1985; Lucansky and White, 1974, 1976; Nishida, 1984; Ogura, 1927, 1972).

A second species, *Hymenophyllopsis asplenioides* A.C.Sm. was established in 1931 (Smith, 1931). The author noted Goebel's view of a potential relationship with the Polypodiaceae *sensu lato* rather than Hymenophyllaceae. Gleason (1931) commented that the genus "probably belongs with the tribe Davallieae" (of the Polypodiaceae). This potential placement was disputed in a subsequent review of the Goebel paper by Morton, where *Hymenophyllopsis* remained "of doubtful affinity" (Morton 1932). The lack of a family level taxon for these species was initially remedied by Christensen (Christensen, 1938). He first established the family Hymenophyllopsidaceae, although the required Latin description of the family was only provided much later by Pichi-Sermolli (1970). Christensen noted once again that scale and sporangial characters were reminiscent of those of Cyatheaceae. He concluded, however, that the Hymenophyllopsidaceae, with its unique combination of characters, was clearly different from the Hymenophyllaceae, Cyatheaceae, and Polypodiaceae *sensu lato*. Christensen placed the family Hymenophyllopsidaceae in his system between the families Loxsomaceae (=Loxomataceae) and Plagiogyriaceae (Christensen, 1938). Copeland (1947) regarded *Hymenophyllopsis* as a fern of "Pteridaceous ancestry", but indicated that "in ignorance of its proper position" he was unable to place it more definitely in his own system.

Goebel's original anatomical data were supplemented by additional observations by Vareschi (1958), which accompanied the description of a third named species: *H. universitatis* Vareschi. In this study, the Hymenophyllopsidaceae were again considered to be "one of the most problematic of all ferns", and no attempt was made to relate the family to any other ferns. It was proposed that the three species "represent isolated relicts of numerous species, extinguished in former times" (Vareschi, 1958). A fourth species, *H. steyermarkii* Vareschi, was subsequently described (Vareschi, 1966), and all then-known species were included in the description of the family Hymenophyllopsidaceae for the Flora of Venezuela (Vareschi, 1969). There the family was listed between the families Hymenophyllaceae and Davalliaceae, but it is not clear that this placement represented any statement about family relationships.

Data on spore structure further distanced the family from the Hymenophyllaceae (Tryon and Tryon, 1982). Those authors suggested that the genus is "probably related to the ancestors of *Dennstaedtia*".

In 1973, *Hymenophyllopsis hymenophylloides* Gómez was described (Gómez, 1973), and three additional new species were described in 1984 (Lellinger, 1984). Lellinger commented that the species more closely resemble those of *Hymenophyllum* than they do other ferns, but further noted that they have some characters that resemble those of the Cyatheaceae. As a result, by 1984 a total of eight species of *Hymenophyllopsis* had been described, but still the family remained in uncertain placement among the ferns.

In addition to the scale and sporangial characters that led earlier researchers to compare Hymenophyllopsidaceae with Cyatheaceae, characters from spore ultrastructure provided additional data that indicated "the blechnoid exospore and perispore were characteristic of . . . derived families like the Dicksoniaceae and Cyatheaceae" (Tryon and Lugardon, 1990). These comments were, however, qualified by the observation that "the highly dissected leaves of *Hymnenophyllopsis* and the bivalvate indusium . . . are not characteristic of the Cyatheaceae", and "relationships with other American genera are obscure" (Tryon and Lugardon, 1990).

It is clear, however, that the spores of (the former) *Hymenophyllopsis* do resemble the verrucate spores of certain species of *Cyathea*. For example, spores of *Cyathea furfuracea* (Fig. 21 of Tryon, 1976) compare with those of *H. hymenophylloides* (Fig 81.1 of Tryon and Lugardon, 1990). Similarly, spores of *Cyathea divergens and C. delgadii* (Figs. 27 and 28 of Tryon, 1976) resemble those of *H. asplenioides* (Figs. 81.3 and 81.4 of Tryon and Lugardon, 1990).

The problematic placement of Hymenophyllopsidaceae was again emphasized by Kramer (1990) and Kramer and Lellinger (1990), who stated that *Hymenophyllopsis* was a genus without known relatives, and that it was among the few fern genera that "in my opinion cannot at all be satisfactorily accommodated within the framework of leptosporangiate families. *Hymenophyllopsis* is definitely not related to Hymenophyllaceae but may be not too far away from Dennstaedtiaceae."

In the most recent taxonomic treatment of the Hymenophyllopsidaceae (Lellinger, 1995), which included all eight currently recognized species, the affinities of the family remained problematic. Although reference was again made to dennstaedtioid ferns and the Hymenophyllaceae, there were no strong conclusions concerning the affinities of the Hymenophyllopsidaceae with other families of ferns.

The "genus" *Hymenophyllopsis* has long considered to be an isolated family Hymenophyllaceae, and was even classified in its own order Hymenophyllopsidales Pic.Serm. ex Reveal (Reveal, 1993). As previously noted, molecular studies have shown that *Hymenophyllopsis* actually belongs either within or sister to the New World clade of lineages of the genus *Cyathea s.s.* (Cyatheaceae) (Korall, *et al.*, 2007; Janssen *et al.*, 2008). Accordingly, new combinations and name changes were made by Christenhusz (2009), so that all species formerly classified as *Hymenophyllopsis* now have valid names as *Cyathea* species. He named the group as a separate "subgenus *Hymenophyllopsis*" within *Cyathea,* but this is in the absence of an accepted infrageneric classification for the rest of the genus.

In view of the apparent large morphological and anatomical differences between "*Hymenophyllopsis*" and more typical *Cyathea* species, despite their close phylogenetic relationships, we undertook a study to compare the anatomy and development of *Hymenophyllopsis* species with that of other *Cyathea* species. In particular, we compare the relatively diminutive *Hymenophyllopsis* species with the distinctive early "young sporophyte" stages of typical *Cyathea* tree fern species. Young tree fern sporophytes have long been known to differ anatomically from the complex adult plants (Lucansky and White, 1976; Stephenson, 1907).

MATERIALS AND METHODS

Samples of young sporophytes and adult specimens of *Cyathea multiflora* Sm. and *C. trichiata* (Maxon) Domin were obtained from field collections. *Cyathea multiflora* and *C. trichiata* were selected as good representative species for the diversity of New World *Cyathea.* Both are familiar common species of tree ferns. *Cyathea multiflora* represents a large group of species (the *C. gibbosa* group) many of which have scattered sclerenchyma strands throughout the ground tissues of the stem. *Cyathea trichiata* is representative of a major group (the *C. armata* group) of tree ferns with prominent cortical bundle systems in the stem.

Samples of mature sporophytes of the eight species of the former genus *Hymenophyllopsis* were obtained from herbarium specimens with permission, and from field-preserved material. The following species and specimens were included in this study:

Cyathea multiflora Sm.—(White 200207, DUKE)
Cyathea trichiata (Maxon) Domin.—(White 199904, DUKE)

Hymenophyllopsis asplenioides A.C.Sm. (= *Cyathea asplenioides* (A.C.Sm.) Christenh.).—(Holst, Liesner & Steyermark 2901, VEN; Steyermark 93833, NY; Steyermark, Huber & Carreño 128835, MO).

Hymenophyllopsis ctenitoides Lellinger (= *Cyathea ctenitoides* (Lellinger) Christenh.).—(Beitel 85171, NY; Liesner 25279, US; Nozawa *et al.*, 1904, VEN; Steyermark 75855, US).

Hymenophyllopsis dejecta (Baker) Goebel (=*Cyathea dejecta* (Baker) Christenh.).—By this we mean the name as used by subsequent authors and not by Goebel; it appears plain to us that Goebel's species is actually the same as *H. ctenitoides*, and is not Baker's species. (Liesner 23179, MO; Vivas *et al.*, 3014, VEN).

Hymenophyllopsis hymenophylloides L.D.Gómez (= *Cyathea hymenophylloides* (L.D.Gómez) Christenh.).—(Fernández & Aymard 4873, VEN; Maguire 32895, DUKE; Steyermark 58216, Mo; Steyermark 92730, VEN).

Hymenophyllopsis incognita Lellinger (= *Cyathea incognita* (Lellinger) Christenh.).—(Steyermark & Wurdack 1141, VEN).

Hymenophyllopsis steyermarkii Vareschi (= *Cyathea tepuiana* Christenh.).—(Liesner 17989, MO, VEN; Liesner, 25165, MO; Steyermark 93963, VEN; Steyermark 103893; Steyermark, Huber & Carreño 128605, MO).

Hymenophyllopsis superba Lellinger (= *Cyathea trichomanoides* Christenh.).—(Beitel 85314, US; Liesner & Carnevali 22432, MO).

Hymenophyllopsis universitatis Vareschi (= *Cyathea universitatis* (Vareschi) Christenh.).—(Holst 3697, MO; Steyermark 94041, VEN; Steyermark *et al.*, 116030, VEN).

Dried herbarium material was rehydrated with strong detergent solutions, processed through a tertiary-butyl-alcohol (TBA) series, and embedded in paraffin. Gum elemi was added to the paraffin mixture to improve its hardness and sectioning properties. Serial 10µm sections were stained with safranin and fast green (Johansen, 1940). Field-collected specimens were preserved in formalin acetic alcohol (FAA). Samples were subsequently dehydrated in a TBA series, embedded in paraffin, sectioned and stained. Freehand sections of other materials were mounted in glycerin solutions. Sections of large stems of mature *Cyathea* plants were made with the use of a macrotome (Lucansky, 1976b).

Photographs of entire plants, large stem sections, whole mounts and stained sections were taken with a Canon PowerShot S3IS camera. Vouchers are deposited in the Duke herbarium (DUKE) and others as noted.

RESULTS

General description of Hymenophyllopsis species.—Throughout most of the following descriptions we will continue to refer to these species under their *Hymenophyllopsis* binomials to simplify comparing them with more typical *Cyathea* species.

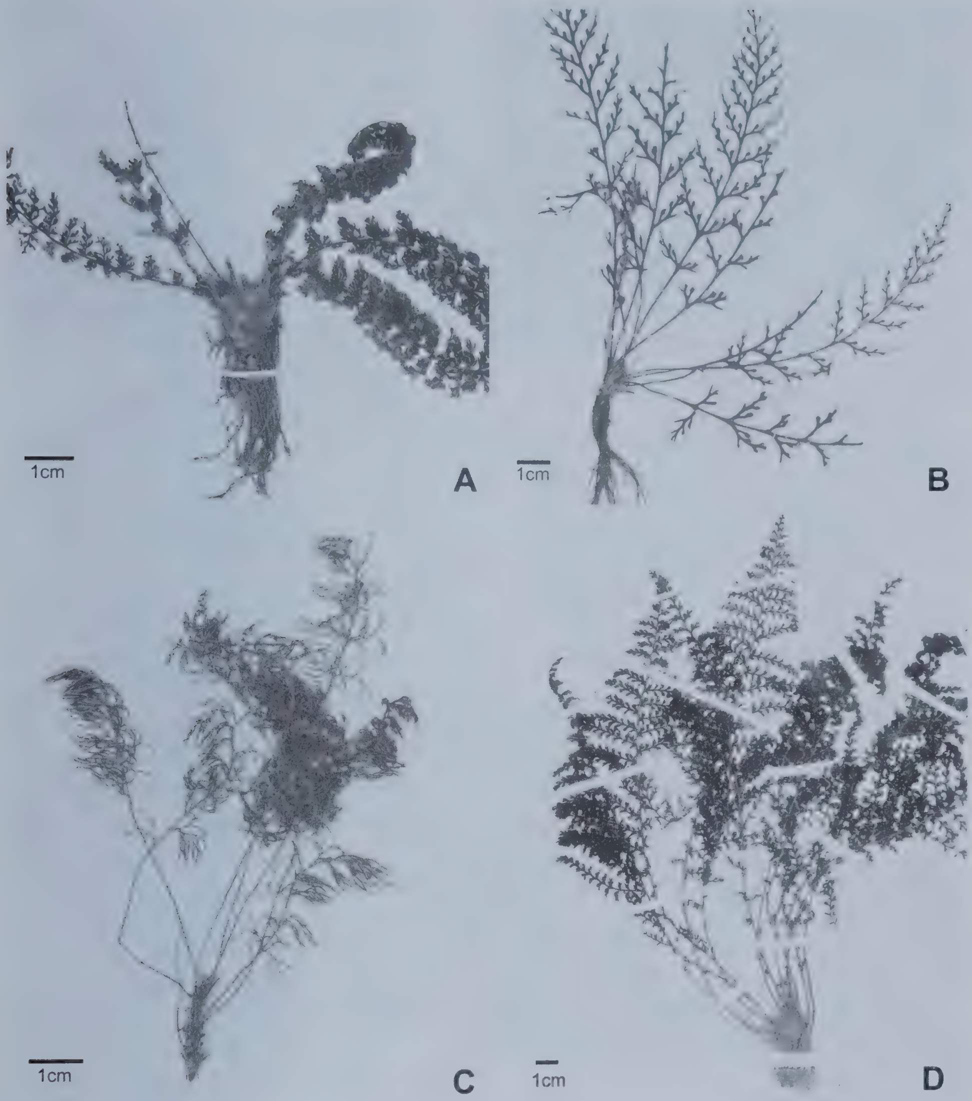

FIG. 1. *Hymenophyllopsis* species, showing variations in growth form. (A) *H. ctenitoides* (Beitel 85171, NY), with erect stem and terminal cluster of leaves comparable to tree ferns. (B) *H. asplenioides* (Steyermark, Huber, & Carreño E. 128835, MO), a form with almost "bladeless" leaves. (C) *H. steyermarkii* (Liesner 17989, VEN), a species with slender stems and more elongate internodes. The specimen is of the unusual terete-lobed form of the species. (D) *H. universitatis* (Steyermark 66195, VEN), a large specimen with stout-appearing stem covered by long scales.

Hymenophyllopsis species are a group of small to very small ferns that are terrestrial or more commonly epipetric in rock crevices. Most of these species have erect stems with closely crowded nodes, often reminiscent of a tiny tree fern up to several centimeters tall (Fig. 1A-D). *Hymenophyllopsis hymenophylloides*, however often has creeping, slender stems with elongate internodes, and *H. steyermarkii* (Fig. 1C) commonly also has elongate internodes on slender erect stems. Stem diameters can be up to approximately 5mm (e.g., *H. ctenitoides*, Fig. 1A), but other species are much more slender (less than 2mm in *H. hymenophylloides*). Stems of most species appear much stouter with associated scales, petiole bases and roots, to ca. 2cm in *H. ctenitoides* and *H. universitatis* (Fig. 1D).

Roots are present on the stem surface, generally one per node, growing downward from the leaf bases. Leaves are generally in a terminal tuft or crown of fronds, and are up to ca. 30 centimeters long in the largest individuals (e.g., in *H. dejecta*), the petioles range from very short (e.g., *H. superba*) to long (e.g., *H. dejecta*). Petioles are extremely slender (less than 0.5mm diameter) in *H. hymenophylloides* but may be up to 2mm diameter in *H. dejecta*.

Leaf blades are typically 2- 3 pinnate-pinnatifid, mostly highly dissected into linear single-veined ultimate segments, but *H. universitatis* has coarser dissection than the others (Fig. 1D). The blades of the pinnae and pinnules are arranged in the same plane as the frond in most species, but they are typically rotated, pendent, and forming a somewhat 3-dimensional frond architecture in *H. dejecta* and *H. steyermarkii* (Fig. 1C).

The sori appear to be marginal, and terminal on a lobe and vein. The vein often branches to extend beyond the sorus. The indusia appear to be bivalved, with a pouchlike inner indusium and a matching outer indusial valve; the adaxial valve corresponds to a lobe of the leaf margin. The indusial margins range from (sub)entire (*H. universitatis*) to strongly lobed and lacerate (*H. hymenophylloides*). Indusia are persistent following the shedding of the spores and sporangia, and anatomically resemble the lamina of the leaf. Sporangia are few and relatively large. Spores are trilete, globose to triangular, and verrucose.

Anatomy of Hymenophyllopsis species.—The eight *Hymenophyllopsis* species are surprisingly diverse in external shoot morphology, and also vary in the dissection and appearance of the leaf blades and in details of the sori. In contrast, the internal anatomy of their stems, leaf axes and leaf blades are basically similar. Stems of *Hymenophyllopsis* species have a single-layered epidermis of relatively thick-walled cells. Scales are present, especially at the stem apex and on the petiole bases; the scales range from short and broad (*H. steyermarkii, H. hymenophylloides*) to long and linear (*H. ctenitioides, H. universitatis*).

The cortex in all species is zoned (Fig. 2A, B). The outer cortex of most species is composed of thick-walled parenchyma cells. The inner cortical zone is composed of thin-walled parenchyma cells. *Hymenophyllopsis hymenophylloides* differs from the others in having a cortex that has thin-walled outer cortical parenchyma and thick-walled inner cortical cells. Following the youngest stages of stem development, older stem regions of *H. universitatis* have a cortex composed of uniformly thick-walled parenchyma cells. The ground tissue of the stem in *Hymenophyllopsis* species is strictly parenchymatous. Sclerenchyma zones and secretory cells are absent. Aerophores and petiolar abscission plates are absent from *Hymenophyllopsis* stems.

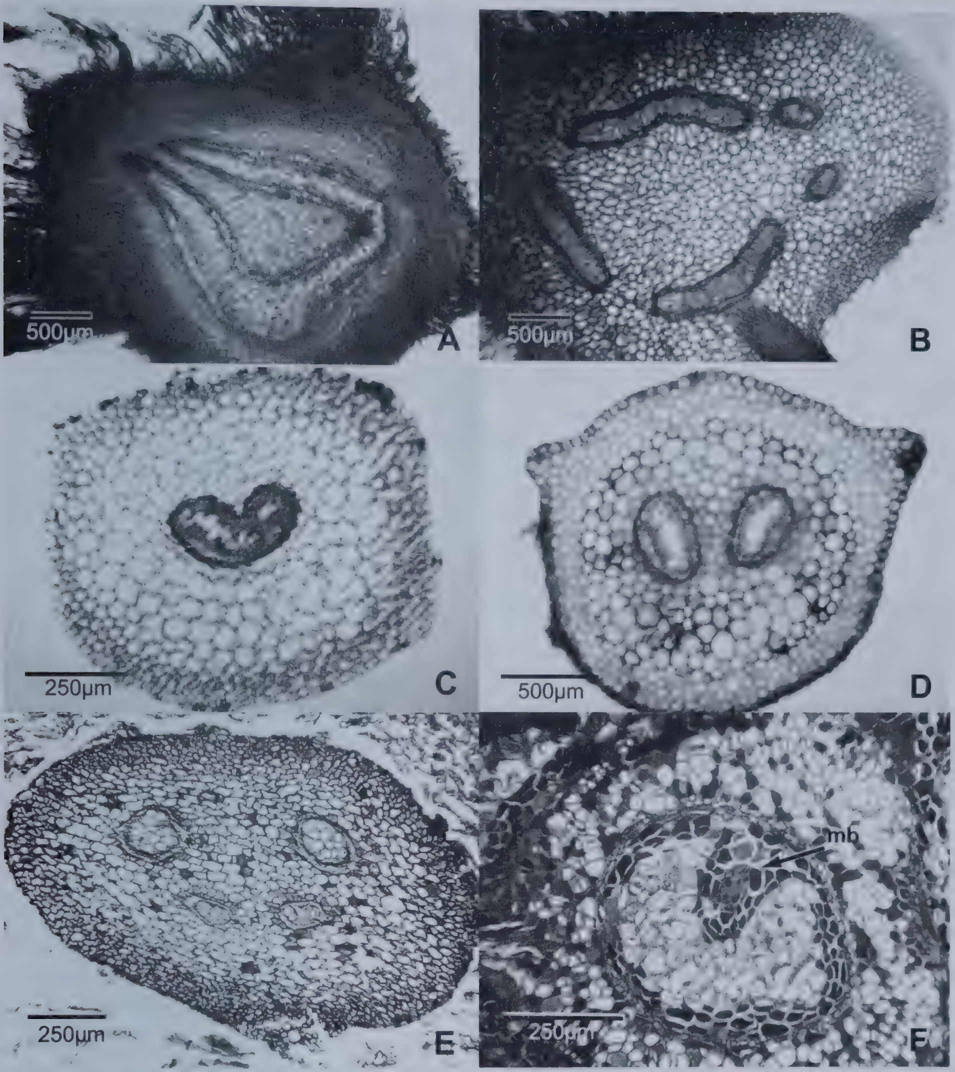

FIG. 2. Anatomy of *Hymenophyllopsis*: (A) *H. ctenitoides* (Nozawa *et al.*, 1904, VEN), section of stem at a level showing a single leaf gap with two departing traces at upper left. (B) *H. dejecta* (Vivas *et al.*, 3014, VEN), section of large adult plant showing a dictyostele with three leaf gaps and two departing leaf traces. Stem histology is very simple. (C) (*H. universitatis* Holst 3697, MO) Petiole with one vascular bundle. (D) Petiole of *H. ctenitoides* (Nozawa *et al.*, 1904, VEN) with two vascular bundles. (E) Petiole of *H. superba* (Liesner & Carnevali 22432, MO) with four vascular bundles, the most complex pattern seen among any *Hymenophyllopsis* species. (F) Detail of unusual stem of *H. ctenitoides* (Beitel 85171, NY), showing the origin of a single medullary vascular bundle (mb).

In species such as *H. asplenioides, H. ctenitoides* (Fig 2A), *H. dejecta* (Fig. 2B), and *H. universitatis*, the pith is composed of uniformly thin-walled parenchyma cells, whereas in *H. hymenophylloides* and *H. superba* the pith consists of thick-walled cells. In some samples of *H. ctenitoides* and *H. dejecta* there are small clusters of thick-walled cells among the parenchyma. Although secretory cells are absent, tannin-filled cells may be dispersed throughout the pith in *H. ctenitoides*.

A protostele characterizes the vascular pattern in the most proximal portion of the stem. Serial sections from the base of a young plant show a sequential change in stelar pattern from protostele to solenostele (Fig. 2A). At the most proximal, protostelic level of the stem, a single U-shaped leaf trace departs from the stele to the leaf with no gap in the vascular cylinder. In more distal sections, the stem stele is a solenostele with a single leaf gap in any given cross section (Fig. 2A). In distal regions of older plants, a typical dictyostele occurs with as many as three or four gaps in a cross section (Fig. 2B). These are typical fern leaf gaps: the parenchyma cells of the pith and the cortex are continuous through a gap in the stele, and the external and internal endodermis is continuous around the margins of the gap. At every node of the stem, a single lateral root arises from the stele immediately proximal to the opening of the leaf gap and the origin of the leaf traces.

Most stems of *Hymenophyllopsis* species lack any evidence of medullary vascular bundles. However, in two stems, both *H. ctenitoides*, a simple medullary vascular bundle system was observed (Fig. 2F). In sequential sections of one of the two specimens there were nine medullary bundles. There were cross sections in which two medullary bundles were present at the same level, but the other bundles occurred singly. One pair of bundles originated independently, fused for a short distance, and separated again before each ended blindly. Apart from that one example of observed fusion between bundles, each of the medullary bundles originated and terminated independently of the other bundles, and none connected to the main stele.

The anatomy of the medullary bundles was generally uniform; their complexity was dependent on the number of cells that composed the bundle (Fig. 2F). In the largest medullary bundle, a dark-staining layer of cells encloses a layer of thin-walled parenchyma cells. Internal to this is another layer composed of similarly dark staining cells. A single layer of thin-walled parenchyma is subjacent to this latter cell layer. The central core of the medullary bundle is composed of 3 to 6 thick-walled fibers. The thick-walled cells in the later-formed medullary bundles are tracheids with scalariform wall thickenings. The smaller medullary bundles have a similar organization, but were composed of fewer cells.

In the second stem, a single medullary bundle was observed to arise proximally as a small proliferation or outgrowth of the inner endodermal layer of the stele (Fig. 2F). Distal to its origin, the bundle became central in the pith and was composed of a central core of xylem cells, surrounded by a few thin-walled parenchyma cells. The entire structure was enclosed in a 2-4 cell layered "endodermis". Distally, the strand becomes reduced in cell number and ended blindly.

An endodermis surrounds each meristele and is composed of cells that are small, thin-walled, and dark-staining (Fig. 2B). A parenchymatous outer pericycle surrounds the phloem, which includes circumferentially elongate tangential cells, other sieve cells, and small thin-walled parenchyma cells. The xylem region of the stele is several-seriate, with numerous dark-staining tannin-filled parenchyma cells among the tracheary elements. Xylem maturation in each meristele is mesarch.

Hymenophyllopsis species differ in the number of leaf traces and petiolar vascular bundles. The first evidence of leaf gap formation appears as a bulge in the stele distal to the departure of a lateral root. In the leaves of young plants and small shoots of all species, a single U-shaped leaf trace departs from the stele and enters the base of the petiole as a single bundle (Fig. 2C). *Hymenophyllopsis aspleniodes*, *H. hymenophylloides, H. incognita* and *H. universitatis* retain single leaf traces and single petiolar bundles as adult plants.

In larger plants of the other *Hymenophyllopsis* species, prior to fully detaching from the stele, the U-shaped leaf trace divides into two separate strands, and a two-trace pattern develops. The gap in the stele closes, and two separate traces enter the base of the petiole. In larger, later-formed leaves of older plants of these species, two separate traces, one from each arm of the gap, depart from the stele to the petiole base, and the petioles have two vascular bundles (Fig. 2A, D). *Hymenophyllopsis ctenitoides* and *H. dejecta* consistently have two petiolar vascular bundles as large adult plants. A few large petioles of *H. ctenitoides* show further subdivision of the petiolar bundles to form a maximum of three bundles. In large plants of *H. universitatis* there may be either one or two petiolar vascular bundles but most plants retain a single petiolar bundle.

In large plants of *H. superba* there are four leaf traces, two traces departing from each side of the gap, and there are four vascular bundles in the petiole (Fig. 2E). This is the most complex leaf trace/petiole bundle arrangement found in any *Hymenophyllopsis* species.

Petioles of *Hymenophyllopsis* species have a single-layered epidermis composed of thick-walled parenchyma cells. Immediately subtending the epidermis is an outer zone of several cell layers of thick-walled parenchyma cells. The bulk of the petiole, internal to the outer zone, is composed of thinner walled parenchyma cells (Fig. 2C, D). There may be some thick-walled parenchyma immediately surrounding the petiolar vascular bundles (e.g., in *H. dejecta*). Secretory strands are absent in the petioles of all species.

The leaf blade anatomy of *Hymenophyllopsis* species is extremely simple (Fig. 3A, B). There is a single-layered upper and lower epidermis of thin-walled parenchyma cells. There are no stomata. The mesophyll is composed of one to three layers of large, vacuolated, thin-walled parenchyma cells. Intercellular spaces are very small or lacking. There is a single centrally located vascular bundle in each lobe of the blade. All of the parenchyma cells

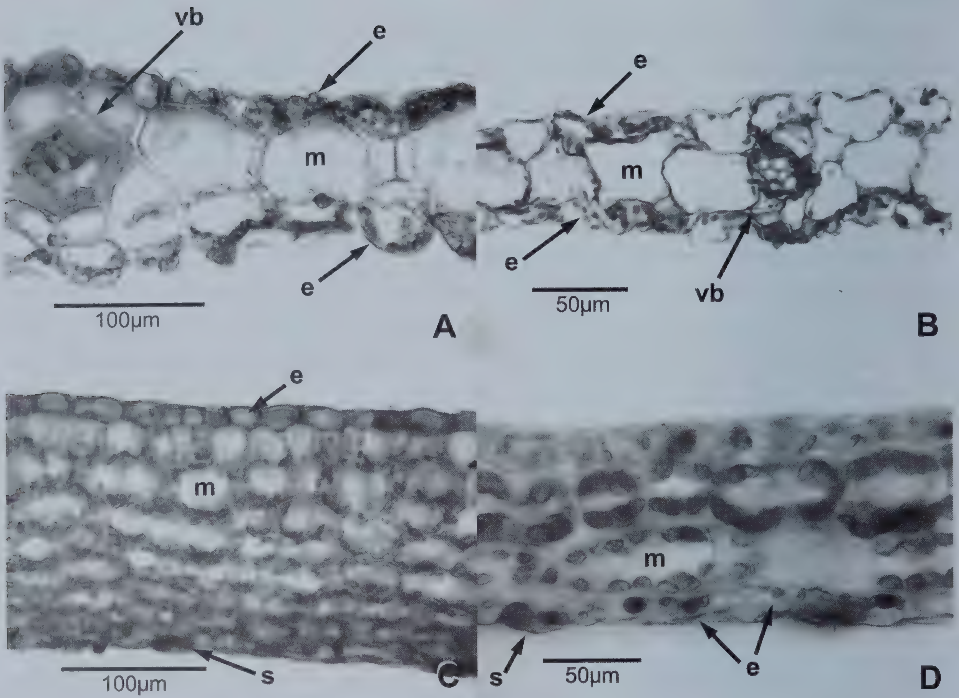

FIG. 3. Cross sections of leaf blades of *Hymenophyllopsis* species and *Cyathea schiedeana*. (A) *H. ctenitoides* (Nozawa *et al.*, 1904, VEN), and (B) *H. superba* (Liesner & Carnevalli 22432, MO). Upper and lower epidermal cells with numerous chloroplasts, the mesophyll consisting of one or two cell layers of large, vacuolate thin-walled cells with few chloroplasts. Stomata and intercellular spaces are lacking. (C, D) *C. schiedeana* (White 200206 DUKE). (C) Leaf of adult plant. Epidermal cells lack chloroplasts other than in stomatal guard cells of the lower epidermis. Mesophyll consists of seven or more layers of cells with many chloroplasts. (D) Young sporophyte leaf. Epidermis cells with prominent chloroplasts, and mesophyll of just two cell layers of thin-walled parenchyma cells. Stomata and intercellular spaces are present. e, epidermis; m, mesophyll; s, stomate; vb, vascular bundle.

of the leaf contain chloroplasts, with the greatest abundance of them in the cells of the epidermis. Some *Hymenophyllopsis* species have bands of tannin-filled cells in the leaf epidermis. Leaf blades of *H. hymenophylloides and H. surperba* are especially thin, with only one or two layers of mesophyll cells.

Several collections (Liesner 17989, MO, VEN; Steyermark 93963, VEN; Steyermark 103893, MO; Steyermark, Huber & Carreño 128605, MO), otherwise corresponding well to *H. steyermarkii* have a distinctive lamina morphology with terete lobes (Fig. 1C). This unusual form, with its completely cylindrical leaf blades, and the more typical flat-bladed form of *H. steyermarkii,* otherwise have similar stems, stem anatomy, scales, and sori.

In all species except *H. superba*, each pinna is vascularized by a single pinna trace from a rachis bundle. In the rachis of *H. superba*, the four petiolar bundles fuse laterally to form an adaxial and an abaxial bundle. In contrast to all other species, each pinna is vascularized by two traces, one from the adaxial and one from the abaxial bundle.

There is variation in root anatomy among *Hymenophyllopsis* species, especially in the organization of the root cortex.

Roots have a single-layered epidermis. Epidermal cell walls are thick in some species (*Hymenophyllopsis asplenioides, H. ctenitoides* and *H. incognita*), and may be tannin-filled. Other species have an epidermis of thin-walled cells (*H. dejecta, H. hymenophylloides, H. steyermarkii, H. superba* and *H. universitatis*). Subjacent to the epidermis is a layer of very thick-walled parenchyma cells (*H. asplenioides, H. ctenitoides, H. hymenophylloides, H. steyermarkii,* and *H. universitatis*). In *H. ctenitoides* this layer may be single or double; in the other species it is a single layer. The other three species lack this distinct cell layer (*H. dejecta, H. incognita*, and *H. superba*). Some roots of *H. superba* have a row of thin-walled parenchyma subjacent to the epidermis; *H. dejecta* and *H. incognita* have thick-walled subepidermal cells that resemble the rest of the outer cortex.

In some species, internal to this layer of cells the cortex is zoned: an outer cortical zone composed of thick-walled cells and an inner zone of thin-walled parenchyma cells (*H. asplenioides, H. hymenophylloides,* and *H. superba*). In other species, the cortex shows no zonation and is composed of uniformly thick-walled cells that are frequently tannin-filled. (*H. dejecta, H. ctenitoides, H. steyermarkii* and *H. universitatis*). This lack of zonation is also seen in some roots of *H. hymenophylloides*, and *H. superba*. In *H. incognita* the root cortex shows a gradation from thick-walled cells in the outermost layers of cells to thinner- walled parenchyma surrounding the central vascular cylinder.

The xylem pattern of the root in *Hymenophyllopsis* species is typically diarch, but monarch and triarch roots were also observed. Xylem maturation is exarch.

Hymenophyllopsis sori and spores.—In addition to data on the comparative anatomy of mature sporophytes of *Hymenophyllopsis*, several other features were examined.

A bivalved indusium characterizes the sorus of each of the species, and details were variable among the species (Fig. 4A-E). Sori appear to be marginal with an inner and outer indusium. We interpret the outer indusium to represent a modified leaf lobe, whereas the pouch-like inner indusium corresponds most closely to the hemitelioid indusia found in many *Cyathea* species (Fig. 4F).

The average number of sporangia in the sori of each *Hymenophyllopsis* species was quite variable. These numbers ranged from low counts of one to five sporangia per sorus, as in *H. hymenophylloides* (Fig. 4A, 4C) through more than five but fewer than ten sporangia, as in *H. asplenioides, H. ctenitoides* (Fig. 4E), *H. incognita,* and *H. superba*. In *H. dejecta* and *H. universitatis* (Fig. 4B) there are between ten and fifteen sporangia, and *H. steyermarkii* (Fig. 4D) has sporangial numbers slightly in excess of twenty.

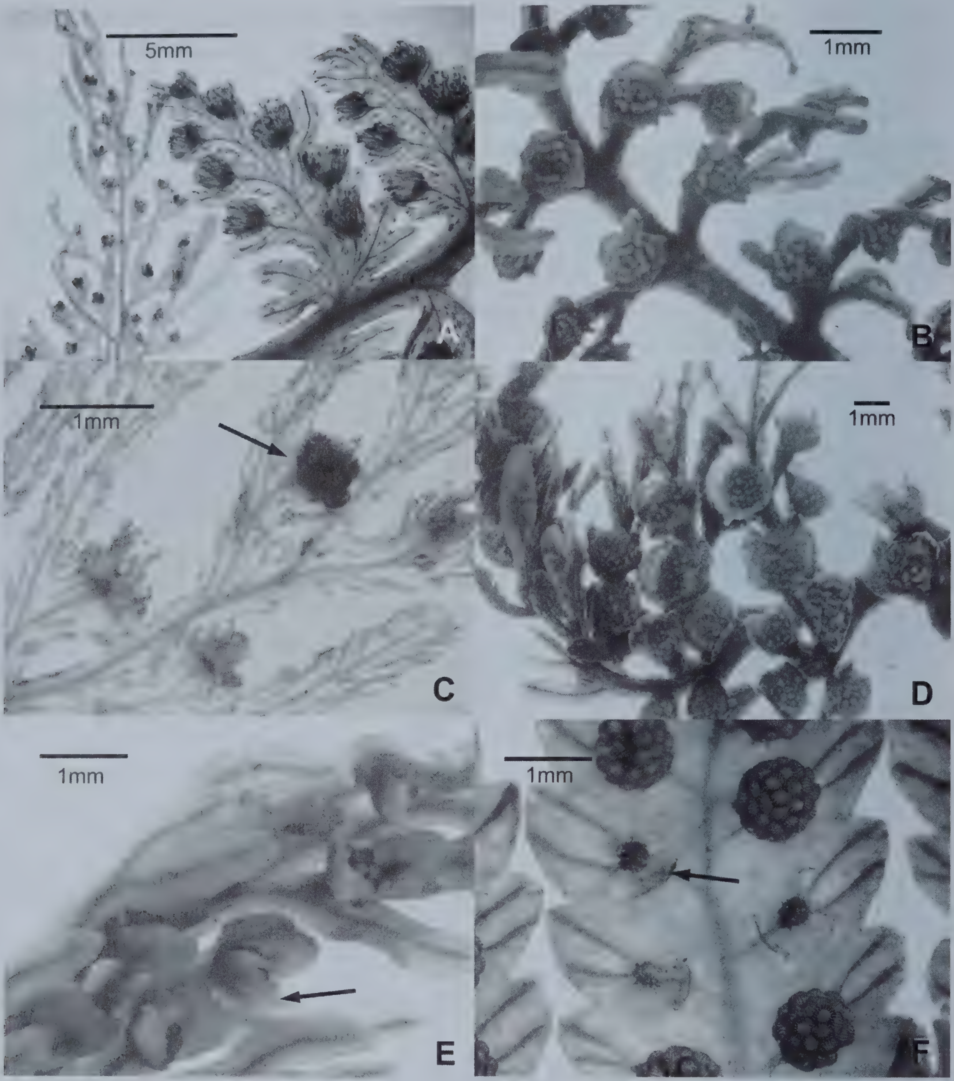

Fig. 4. Sori of *Hymenophyllopsis* spp. and a typical *Cyathea* species: (A) Comparison of extreme soral forms of *Hymenophyllopsis*: Left: *H. hymenophylloides* (Fernández & Aymard 4850, MO) with tiny sori and slender frond lobes, and right: *H. universitatis* (Steyermark 93978, VEN) with much larger sori and coarser leaf dissection. (B) Sori *of H. dejecta* (Vivas *et al.*, 3014, VEN), with cup-shaped indusia enclosing sporangia. (C) Detail of *H. hymenophylloides* with deeply lobed indusia, and only 1-5 sporangia per sorus (arrow). (D) Sori of *H. steyermarkii* (Steyermark & Delascio 129211, MO) with bivalved indusia enclosing numerous sporangia. (E) *H. ctenitoides* (Nozawa *et al.*, 1904, VEN) small sori with inner indusia (arrow) approaching hemitelioid indusia of many *Cyathea*. (F) Sori of *Cyathea multiflora* (White 200207, DUKE), with numerous sporangia; three sori with sporangia removed to show hemitelioid indusia (arrow).

Of the eight species, five are characterized by having 32 spores per sporangium *(H. asplenioides, H. incognita, H. steyermarkii, H. superba and H. universitatis)*. The other three species *(H. ctenitoides, H. dejecta and H. hymenophylloides)* have 64 spores per sporangium. The species with 32 spores per sporangium had somewhat larger-sized spores than those with 64 spores per sporangium. *H. hymenophylloides* (64 spores per sporangium) had the smallest spores and *H. asplenioides* and *H. incognita*, both with 32 spores per sporangium had the largest spores. The species with the fewest sporangia per sorus is one of the 64-spored species, *H. hymenophylloides*, whereas *H. steyermarkii*, a species with 32 spores per sporangium, had the most sporangia per sorus.

Sporangium size ranged from the smallest found in *H. superba*, to larger ones including *H. asplenioides, H. incognita, H.steyermarkii* and *H. universitatis*. All of these species have 32 spores per sporangium. Intermediate-sized sporangia characterized *H. ctenitoides, H. dejecta* and *H. hymenophylloides*, the three species with 64 spores per sporangium. *Hymenophyllopsis* sporangia were somewhat larger than sporangia of other *Cyathea* species (ranging appx. 300-500μm in length vs. 200-350μm). Spore sizes are similarly larger (ranging appx. 10-12.5μm diameter vs. 7.5-10μm).

Anatomy of adult plants of typical Cyathea species.—Typical *Cyathea* species exhibit highly complex stem and leaf anatomy.

Cyathea multiflora Sm.—This species is a tree fern that may grow to 5m in height and 5-8cm in trunk diameter. Leaves may reach 2.2m in length. The stems and leaf bases are covered with abundant and complex scales.

The stem anatomy of adult plants of *C. multiflora* Sm. is highly complex (Fig. 5A, B). At the apex of the shoot, the epidermis is composed of thin-walled parenchyma cells. Subjacent to the epidermis is a narrow zone a few cells wide composed of thin-walled parenchyma cells. Beneath this is a hypodermis sheath composed of a variable number of rows of thick-walled sclerenchyma. The innermost cells of this sheath are specialized cubical cells. These cells have thickened cell walls on three sides and a thin tangential wall facing the cortical parenchyma. Characteristically, cubical cells contain a silica crystal. The hypodermis is subtended by an inner cortical zone that is composed of relatively homogeneous thin-walled parenchyma cells. There are gaps in the thick-walled hypodermis where aerophores occur on the stem. These gaps are filled with parenchyma cells that connect the outside of the stem to the thin-walled parenchyma of the cortex. As the stem matures, the epidermis disintegrates, and the thick-walled cells of the hypodermis become the outer surface of the stem. There are numerous laticifer strands as well as numerous slender strands of sclerenchyma cells throughout the cortex (Fig. 5B).

The stele of mature stems is a very complex dictyostele with numerous leaf gaps and meristeles in any given cross section (Fig. 5A). A large number of leaf traces arise from the edges of the gap associated with each leaf (Fig. 5B). In this species, numerous roots are formed at the nodes, in association with the leaf

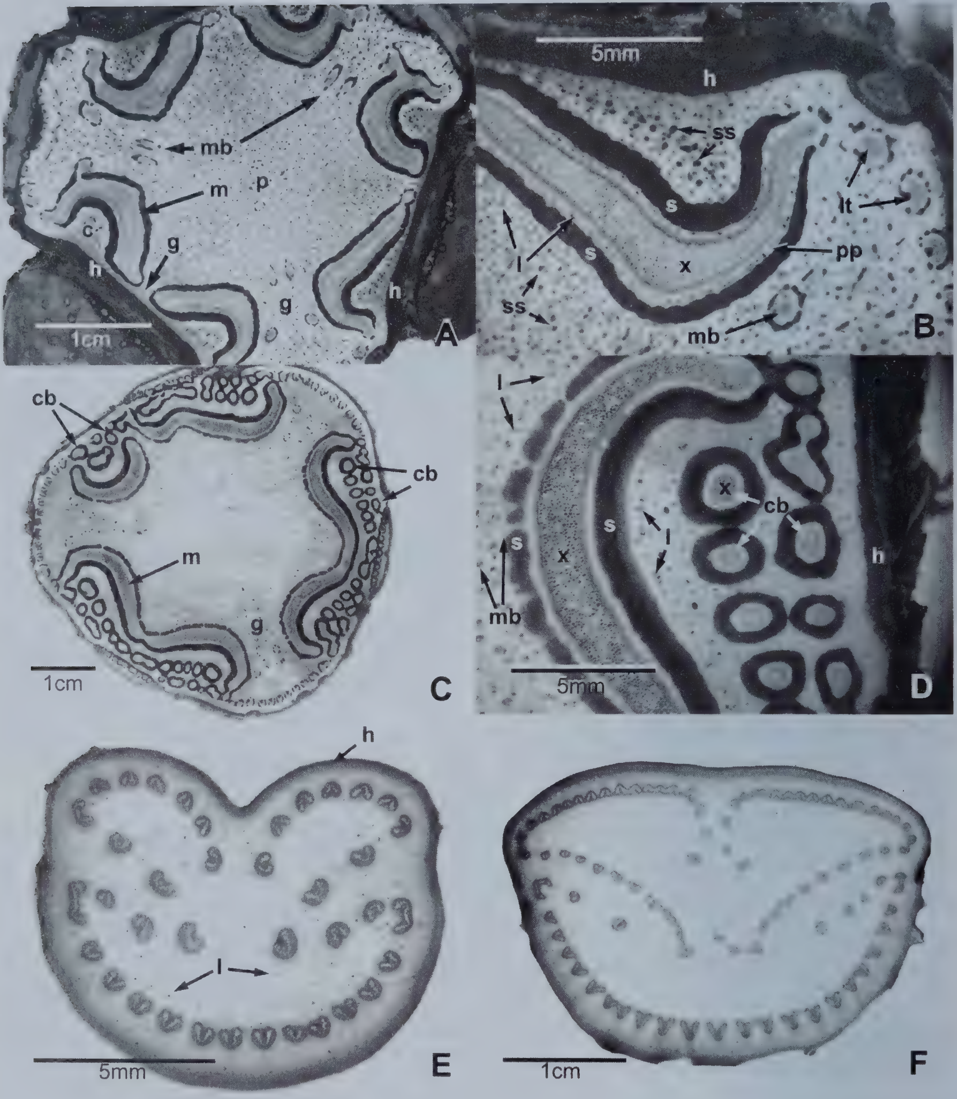

Fig. 5. Stem and petiole anatomy of mature typical *Cyathea*. (A, B, E), *Cyathea multiflora* (White 200207, DUKE). (A) Stem section showing six leaf gaps, numerous medullary vascular bundles, and scattered sclerenchyma strands throughout cortex and pith. (B) Detail showing complex anatomy. (C, D, F), *C. trichiata* (White 199904, DUKE). (C) Stem section showing presence of elaborate cortical vascular bundle system. (D) Detail showing complex stem anatomy and cortical bundles with prominent sclerenchyma sheaths. (E) Complex petiole of *C. multiflora* with numerous vascular bundles and scattered laticifers. (F) Complex petiole of *C. trichiata* with a very large number of vascular bundles. c, cortex; cb, cortical bundle; g, gap; h, hypodermis; l, laticifer; lt, leaf trace; mb, medullary bundle; m, meristele; pp, peristelar parenchyma; p, pith ; s, sclerenchyma sheath; ss, sclerenchyma strands; x, xylem.

bases and stelar gaps. Lateral roots originate from the meristeles below the gaps, from the edges of the gap margins, and from the abaxial leaf traces.

A stelar sclerenchyma sheath composed of multiple layers of fiber-like cells surrounds the meristeles (Fig. 5B). The cell layer of this zone that faces the cortical parenchyma is composed of cubical cells with silica crystals, similar to those associated with the outer hypodermis zone of the cortex.

Between the fibrous sheath and the stele is a distinctive zone of several cell layers of thin-walled parenchyma cells, the peristelar parenchyma zone (Fig. 5B). These cells are smaller than the parenchyma cells of the cortex and pith, there are numerous intercellular spaces and numerous intercellular pectic filaments.

Each meristele has a characteristic structure (Fig. 5B). An endodermis encloses the stele. Beneath the endodermis is the pericycle, and internal to this is a layer of tangential cells. These cells compose a circumferential system of outer phloem cells. A characteristic zone of phloem encloses the core of the meristele. Central to the meristele is a multi-layered xylem core with mesarch xylem maturation.

The bulk of the stem cross section is pith. The zonation of the pith is similar to that of the cortex. The outermost pith zone is peristelar tissue. Subjacent to that is the inner scelerenchyma sheath of each meristele. At the leaf gaps, the pith and cortex are continuous (Fig. 5A, 5B). The bulk of the remainder of the pith is composed of large, thin-walled parenchyma cells. As in the cortex, there are numerous scattered sclerenchyma strands throughout the pith, and laticifer strands are present throughout the pith and peristelar zones.

There is a very complex system of numerous medullary vascular bundles throughout the pith (Fig. 5A, 5B). These bundles branch and fuse with one another and connect with the stele and the leaf traces at the nodes. A ring of sclerenchyma strands forms a broken sheath associated with each of the medullary bundles (Fig. 5B). These strands are similar to the sclerenchyma strands that are scattered throughout the ground tissue of the cortex and pith.

Petioles of adult *C. multiflora* plants have a single layered epidermis composed of thick-walled parenchyma cells. The abundant scales are outgrowths of the epidermis. When these scales eventually break off, they leave behind elevated sclerified bases that form the prominent spines of the petiole base. Subjacent to the petiolar epidermis are a few cell layers composed of thin-walled parenchyma cells. Beneath these cells there is a hypodermis zone several cell layers wide (Fig. 5E) that is composed of long thick-walled fibers. Where aerophores occur, there is a break in the fibrous zone and this gap is composed of thin-walled parenchyma, thus connecting the petiole surface with the parenchyma of the petiole. There are numerous scattered laticifers throughout the parenchyma of the petiole. In large petioles of mature *Cyathea multiflora* plants there are numerous vascular bundles (Fig. 5E). Each vascular bundle is enclosed with a sclerenchyma sheath. Internal to this is an endodermis that encloses the vascular tissue in sequence: phloem, small parenchyma cells and U- or V- shaped xylem bands. There are laticifer strands in the leaf vascular bundles in this species. Vascular bundles in large petioles of mature plants of typical *Cyathea* species are numerous, often 40 or 50 bundles in a cross section (Fig. 5E, 5F). These bundles form distinct adaxial and abaxial arcs of bundles, which in the rachis give rise to separate adaxial and abaxial traces to the pinnae.

At the juncture of the base of the petiole with the stem, there is a distinctive multicellular zone or plate of sclerenchyma tissue. This "abscission plate" forms a sharp boundary that separates anatomically petiolar tissues from the tissues with typical anatomy of the stem.

In leaf blades of mature leaves of older specimens there is a single-layered epidermis. Both the adaxial and abaxial epidermis lack chloroplasts. However, chloroplasts are present in the stomatal guard cells of the abaxial epidermis. There are at least four to five layers of mesophyll parenchyma cells that contain numerous chloroplasts (as illustrated by *C. schiedeana* in Fig. 3C).

The anatomy of the roots of this species varies. In some samples, there is an epidermis composed of thin-walled parenchyma and subjacent to this, the bulk of the root is composed of homogeneous thin-walled parenchyma cells. In others, and more commonly found, the root is composed of a thin-walled epidermis, subjacent to which is a zoned cortex. The outer zone is composed of thick-walled parenchyma cells. Beneath this zone is an inner zone of thin-walled parenchyma cells that constitutes the bulk of the root. An inner-most zone of two or three cell layers of very thick-walled parenchyma cells surrounds the vascular cylinder. In all roots the vascular cylinder is composed of an endodermis surrounding the pericycle and the xylem and phloem. The xylem pattern is diarch with exarch xylem maturation. There are parenchyma-filled gaps in the thick-walled parenchyma sheath opposite the protoxylem points.

CYATHEA TRICHIATA (MAXON) DOMIN.—The general anatomy of this species (Fig. 5C, 5D, 5F,) is similar to that described above for adult plants of *C. multiflora* (Fig. 5A, 5B, 5E). However, *C. trichiata* lacks scattered sclerenchyma strands in the cortex and pith, and most of the medullary bundles lack sclerenchyma bundle sheaths. This species has especially prominent clusters of laticifers throughout the ground tissues; laticifers are lacking from the peristelar parenchyma zones. Most conspicuously, *C. trichiata* has a complex system of cortical vascular bundles (Fig. 5C, 5D) that is lacking in *C. multiflora*.

The cells of the adaxial and abaxial epidermis of the leaves are thin-walled. Stomata are restricted to the abaxial epidermis. The leaf mesophyll is composed of five to six layers of compact thin-walled parenchyma cells with conspicuous intercellular spaces. Chloroplasts are abundant in the mesophyll cells, but are lacking in the epidermal cells other than the guard cells.

The anatomy of the petiole is also similar to that of *C. multiflora*, including the presence of large numbers of vascular bundles (Fig. 5F).

A large number of cortical vascular bundles with prominent sclerenchyma sheaths characterize the stem anatomy of mature plants of *C. trichiata* (Fig. 5C, 5D). These bundles are much larger in diameter than those of the medullary bundle system. The cortical bundles arise as branches from the edges of the meristeles at the leaf gaps. Cortical bundles are of various sizes in cross section; they may fuse with one another, and may divide both radially and tangentially to form a two- or three-seriate reticulate system of interconnected bundles (Fig. 5D). Each cortical bundle is surrounded by a multi-layered sclerenchyma sheath. The outer cell layer of the sheath is composed of small cubical cells most of which contain a silica crystal. Internal to the sclerenchyma sheath is a narrower peristelar zone of several cell layers of thin-walled parenchyma. Where the sclerenchyma sheath is not complete, these parenchyma cells are continuous with those of the ground tissue of the cortex. There is a single-layered endodermis that encloses the vascular bundle. There are two or three cell layers of thin-walled parenchyma cells between the endodermis and a narrow band of phloem. The phloem is separated from the xylem by parenchyma cells. The xylem cylinder has a conspicuous central core of protoxylem and thin-walled parenchyma cells, surrounded by numerous metaxylem cells (Fig. 5D). The composition and morphology of the cortical bundles clearly distinguish them in cross section from leaf traces and from root cross sections in the cortex.

Anatomy of young sporophytes of typical Cyathea species.—In contrast to the differences in anatomy among adult plants, the anatomy of young sporophytes of scaly tree ferns is broadly similar among species.

CYATHEA MULTIFLORA.—In the smallest and youngest sporophytes, the stem at its proximal end appears to be composed of a fusion of successive petiole bases; the actual stem axis is very small. The stem at this stage is characterized by a single-layered epidermis composed of thin-walled parenchyma cells. In some samples, however, the epidermis is composed of thick-walled cells. The cortex is zoned: an outer zone composed of thick-walled parenchyma cells, and an inner zone of thin-walled parenchyma cells (Fig. 6A). There is no sharp boundary with cubical cells between the zones.

At the most proximal levels in young sporophytes, the stelar pattern is a protostele: a pith is lacking and no gap occurs at the departure of the leaf trace. This pattern is succeeded by a solenostele, with the presence of a pith and a single leaf gap in cross section at the departure of a single leaf trace (Fig. 6A). In these gaps, the parenchyma cells of the pith and cortex are continuous through the opening in the stele. The inner and outer endodermis is continuous around the arms of the stele at the gap. The pith is composed of uniformly thin-walled parenchyma cells. This stage is followed by a solenostelic pattern with two leaf traces, and finally with a dictyostele in which there are two to several leaf gaps in a given cross section, and a gradually increasing number of leaf traces to each leaf (Fig. 6B). Xylem maturation is mesarch.

As the young sporophytes grow larger, the anatomy of the developing stem becomes more complex. In older young sporophytes the single-layered epidermis is composed of thick-walled cells, and the cortex becomes strongly zoned: an outer cortical zone of thick-walled parenchyma cells, and a middle zone of thinner-walled cells with numerous laticifers (Fig. 6B). The cells of the

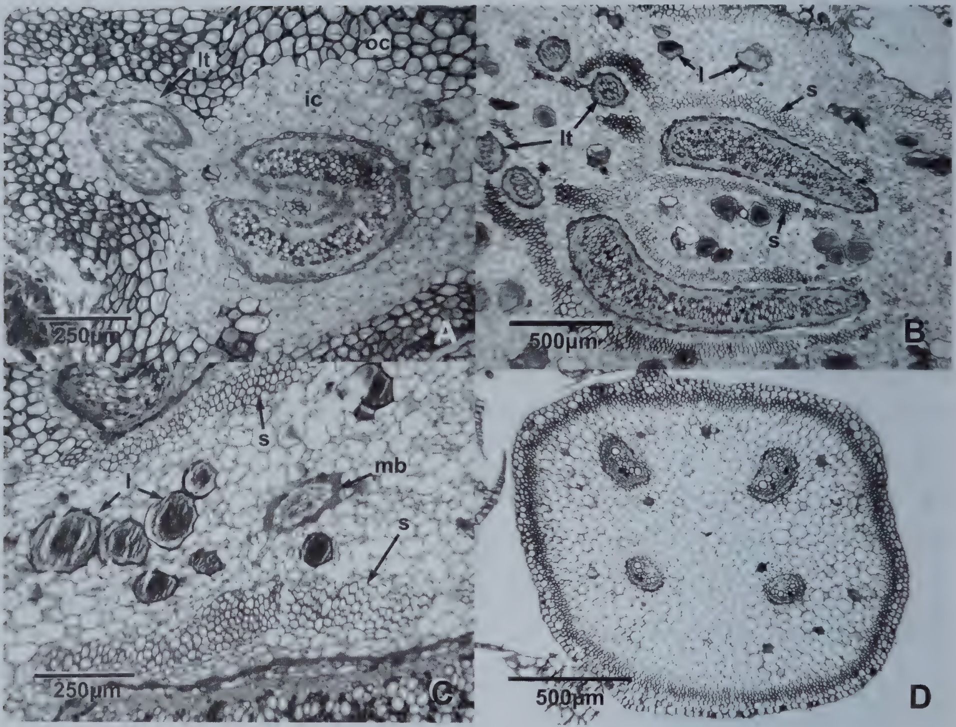

FIG. 6. Anatomy of young sporophytes of *Cyathea multiflora* (199920, DUKE). Section of very young plant with solenostele and single leaf trace per gap. Laticifers, sclerenchyma strands and medullary bundles are absent. (B) Older plant with 2-gap dictyostele and four leaf traces per gap. Medullary bundles absent, but laticifers and stelar sclerenchyma sheaths are present. (C) Pith of older plant showing first medullary bundle (arrow). (D) Petiole of young plant with four vascular bundles per leaf base. ic, inner cortex; l, laticifers; lt, leaf trace; mb, medullary bundle; oc, outer cortex; s, sclerenchyma sheath.

inner zone of the cortex adjacent to the stele form a sclerenchyma sheath and narrow peristelar parenchyma zone. In the pith, the central zone remains parenchymatous with numerous prominent laticifers; the outer zone forms a sclerenchymatous stelar sheath and peristelar zone similar to that in the adult plant (Fig. 6B, C).

Larger young sporophytes have essentially the same zonation of sclerenchyma layers and parenchymatous ground tissue that is seen in adult plants. Laticifers or secretory cell strands occur in the ground tissue of the stem. The first of the scattered sclerenchyma strands in the cortex and pith occur at this stage. Also present at this larger stage are the first examples of aerophore structures and petiolar abscission plates, both of which are absent in younger sporophytes.

Petioles of the leaves of the youngest sporophytes have a single epidermal layer of cells with thickened outer walls, less thick tangential walls and thinner inner cell walls. In the earliest-formed petioles, there is a single subepidermal cell layer of thin-walled parenchyma cells (Fig. 6D). The bulk of these early-formed petioles is composed of uniformly thick-walled cells. In petioles of later-formed leaves, the subepidermal layer of thin-walled cells may be lacking. Subjacent to the epidermis in these later petioles the ground tissue is zoned. There is an outer zone of thick-walled parenchyma cells while the bulk of the petiole is composed of thin-walled parenchyma cells (Fig. 6D). Tannin-filled cells are scattered throughout the ground tissue. In cross sections the petioles of the earliest-formed leaves are characterized by a single vascular bundle. In petioles of subsequent leaves, the vascular pattern becomes increasingly complex; the number of vascular bundles in cross section passing from a single bundle, through stages with two, three and four bundles (Fig. 6B, 6D). The petiolar vascular patterns become increasingly more complex as the young sporophyte approaches adult size (Fig. 5E).

Pinnae of young sporophytes in the one- and the three-petiolar vascular bundle stages are vascularized by a single pinna trace from the rachis bundles. In the four-bundle stage and later, larger leaves, there are double pinna traces, one from each of the adaxial and abaxial bundles of the rachis.

The leaf blade of the first-formed leaves of young sporophytes is characterized by a single-layered adaxial and abaxial epidermis composed of thin-walled cells. Stomata occur in the abaxial epidermis. The earliest leaves of young sporophytes have a mesophyll of only one to two layers of thin-walled parenchyma cells. In the youngest leaves, there are numerous intercellular spaces among the cells of the mesophyll. Chloroplasts occur in the cells of both the epidermis and mesophyll (as illustrated by *C. schiedeana* in Fig. 3D).

The anatomy of the root is variable. Typically, the epidermis of early-formed roots is composed of relatively thick-walled parenchyma cells, except where root hairs occur, and is subtended by a cortex composed of uniformly relatively thick-walled parenchyma cells. Other roots may have an epidermis composed of thin-walled parenchyma cells, that is subtended by a single-cell layer of thick-walled parenchyma cells. The bulk of the cortex may consist of uniformly thin-walled parenchyma cells, or it may be zoned with an outer zone of thick-walled parenchyma cells and an inner zone of thin-walled parenchyma cells. The xylem pattern is typically diarch with exarch xylem maturation. Larger, later-formed roots may have an epidermis composed of thin-walled parenchyma cells, and a cortex that is not zoned, but rather is composed of uniformly thick-walled parenchyma cells. In these larger later-formed roots, the xylem pattern may be triarch. Xylem maturation is exarch.

Medullary bundles first occur in the pith in larger young sporophytes (Fig. 6C). They are absent in the youngest sporophytes and the proximal portions of the stem in older sporophytes. The bundles first appear at the level of the third or fourth leaf gap in the siphonostele of the stem. The earliest medullary bundles first appear *de novo* as clusters of small thick-walled cells surrounded by the larger thin-walled parenchyma of the pith. The earliest bundles extend distally a short distance, remain simple, i.e. few cells in cross section, and end blindly. Subsequent medullary bundles become increasingly complex, extend over longer distances, and fuse with the stele at leaf gaps. In each case, the proximal end of the medullary bundle is a small cluster of thick-walled cells. In serial sections from this simple base, the number of cells composing the bundle increases. There is differentiation of a central core of xylem cells surrounded by parenchyma cells, and the bundle is enclosed in a single-layered endodermal sheath of dark-staining cells (Fig. 6C). In more distal sections, the bundles further increase in cross sectional area with a corresponding increase in the number of cells that compose the bundle. Some bundles had a xylem core of more than eight cells, surrounded by several layers of thin-walled parenchyma enclosed in an endodermal sheath of dark-staining cells. In older and larger young sporophytes, the medullary vascular system becomes increasingly complex. The origin of medullary bundles is clearly associated with leaf gaps and follows the leaf phyllotaxy in sequence. The medullary bundles branch and fuse with one another, and join with the stele and leaf trace system at the nodes.

CYATHEA TRICHIATA.—The anatomy of young sporophytes of this species is largely similar to that described for *C. multiflora*. Very small young plants are solenostelic. As the plants become larger, the stele becomes a dictyostele with several gaps in a given cross section, and up to four leaf traces associated with each gap. The number of traces from the stele to the petiole increases with continued development of the young sporophyte.

The earliest stages of young sporophyte development in this species lack both cortical and medullary bundles. The developmental pattern of medullary bundles in *C. trichiata* parallels that described for *C. multiflora*. Medullary bundles occur much earlier in young sporophyte ontogeny than do cortical bundles. The initial development of the first cortical bundles occurs in much larger, older sporophytes, with stem diameters over 1.5cm.

Histological patterns in the stems, petioles, leaf blades and roots are also comparable to those of *C. multiflora*. As in that species, the earliest stages are very simple and become more complex with increasing age and size. At the base of the sporophytes, the stem has a single-layered epidermis of thick-walled parenchyma cells. Subjacent to the epidermis is an outer cortical zone of thick-walled parenchyma cells and an inner cortical zone of smaller, thinner-walled cells. Sclerenchyma zones, laticifers, aerophore and petiolar abscission plates are absent. As the stem increases in diameter, the zonation of the cortex and pith becomes much more complex, and corresponds to that of the adult plants by the four petiolar bundle stage.

DISCUSSION

Stem and root anatomy of adult plants of Hymenophyllopsis.—The anatomy of the former *Hymenophyllopsis* species is more or less uniform among the eight species. Fully mature, spore-producing plants of all species are very small compared to all other Cyatheaceae; the largest stems may be no more than a few centimeters tall and a few millimeters in diameter. The vascular anatomy of the stem is simple: the most complex dictyostele is characterized by no more than four leaf gaps in a given cross section. In addition, most *Hymenophyllopsis* species completely lack the complex medullary vascular systems that are so characteristic of all more typical *Cyathea* species (e.g., Adams, 1977). However, a very simple medullary bundle system was observed in two stems of *H. ctenitoides*. Cortical vascular bundles are lacking in all species. All *Hymenophyllopsis* species lack a defined stem hypodermis and stelar sclerenchyma sheaths, cubical cells are absent, and none has strands of secretory cells in the stem, leaf axis, or in the vascular bundles of the leaves. Unlike typical *Cyathea*, petiolar abscission plates and aerophores are absent.

The anatomy of the roots is more or less similar in five species of *Hymenophyllopsis* (*H. asplenioides, H. ctenitoides, H. hymenophylloides, H. steyermarkii, and H. universitatis*). The cortex is zoned with an outer zone of thick-walled cells and an inner zone of thin-walled parenchyma cells. This pattern conforms most closely to Schneider's "*Osmunda* type" (Schneider, 1996). The basic patterns in the cortex of the other three species varied. There was no zonation in most of the samples of *H. dejecta*; the cortex is composed of uniformly thick-walled cells. In *H. incognita*, there is a continuous gradation from thick-walled cells to thinner-walled cells from the outer cortex to the inner cortex. The cortex of the most proximal roots of *H. superba* is composed of uniformly thin-walled parenchyma cells. Later-formed roots, however, were of the "Osmunda type" with an outer zone of thick-walled cells and an inner zone of thin-walled cells.

Stem anatomy of adult plants of typical Cyathea.—In contrast to the characteristically simple anatomy of mature, adult *Hymenophyllopsis* species, mature individuals of more typical *Cyathea* species are extraordinarily complex. Both in terms of histology and stelar anatomy, they represent the most complex anatomy of any living pteridophytes. From our broad studies of tree fern anatomy, we know this complexity is true not just for *Cyathea s.s.*, but also for all other genera of Cyatheaceae: *Alsophila, Gymnosphaera,* and *Sphaeropteris.* These genera share a common basic anatomical pattern: stems with a highly elaborate dictyostele, with numerous leaf gaps in a cross section, with elaborate medullary vascular systems, and with characteristic sclerenchyma zones and secretory cells (e.g., Holttum and Sen, 1961; Lucansky, 1976a; Ogura, 1927, 1972; Sen, U. 1964). Cortical bundles are present in some species (e.g., *Cyathea trichiata* and *C. arborea*), but are absent in many others. All of these several hundred species are larger than *Hymenophyllopsis* spp.; the few relatively diminutive species examined (e.g., *Cyathea stolzei* A.R.Sm. ex Lellinger and *Alsophila sinuata* (Hook. & Grev.) R.M.Tryon) still have typical Cyatheaceous anatomy. All possess complex stem anatomy, numerous vascular bundles in the petioles, leaf bases with petiolar abscission plates and aerophore craters.

Comparison of Hymenophyllopsis stems to adult Cyathea and Cyathea young sporophytes.—Although extremely distinct from the complex anatomy of mature adults of *Cyathea*, the anatomy of mature plants of *Hymenophyllopsis* does in fact closely resemble that of young sporophytes of typical *Cyathea* species, both in stelar organization and stem histology. As was noted by Stephenson (1907), young sporophytes of different tree fern species are similar in their basic anatomy. In addition to the *Cyathea multiflora* and *C. trichiata* young sporophytes described here, we have also noted similar anatomical features in young sporophytes of several other *Cyathea* species, as well as similarly young stages of *Alsophila*, *Sphaeropteris* and *Gymnosphaera* species. These young sporophytes are characterized by simple early stages of stelar organization including the typical transitional series from protostele through solenostele to a dictyostele with relatively few gaps in cross section. As in *Hymenophyllopsis*, these early stages of *Cyathea* have one to few vascular bundles in the petiole, and lack medullary and cortical vascular bundle systems in the stem. Histologically, early developmental stages of young sporophytes also lack the well-defined sclerenchyma zones, cubical cells, and strands of secretory cells found in older specimens of *Cyathea*, and other genera of the tree ferns (Holttum and Sen, 1961; Sen, U. 1964).

Comparative leaf anatomy of Hymenophyllopsis and Cyathea.—In *Hymenophyllopsis* species, leaves are very simple: they are small, up to about 30 cm at most, with one or two petiolar vascular bundles (up to four only in *H. superba*). As noted in the earlier descriptions, the leaf blade anatomy of adult plants of this genus is strikingly distinctive (Fig. 3A, 3B). The upper and lower epidermis is composed of small cells that have abundant chloroplasts and represent the main photosynthetic tissue of the plant. Stomata are lacking. The mesophyll, of only one to two cell layers, is composed of large vacuolate parenchyma, with relatively few chloroplasts. Intercellular spaces are not evident.

In contrast, the leaf anatomy of mature adult *Cyathea* plants is complex (Fig. 3C). The fronds are commonly two or more meters long with very complex petiolar and rachis anatomy. Petioles have up to scores of vascular bundles in a cross section. In the leaf blade the cells of the upper epidermis are small and lack chloroplasts. The lower epidermis contains numerous stomata with chloroplasts only in the guard cells. The mesophyll zone has multiple layers of thin-walled parenchyma cells with numerous chloroplasts and prominent intercellular spaces (Fig. 3C) Most New World *Cyathea* species share nectary-like foliar glands (White and Turner 2012); these are completely absent in *Hymenophyllopsis*.

The anatomy of the leaf of very young sporophytes of *Cyathea* species differs from that of the leaves of older plants. Petioles of the first-formed leaves have a single vascular bundle, with two and four petiolar bundle stages in somewhat older young sporophytes. Petioles lack the multiseriate subepidermal parenchyma layers present in the adult plants. The leaf blade anatomy of the earliest leaves of young *Cyathea* sporophytes is also very simple, and different from that of the adult plants. The mesophyll zone is composed of only one to a few layers of parenchyma cells compared to the more complex multiseriate mesophyll of the leaves of adult plants (Fig. 3C, D). In this regard, the leaf anatomy of young sporophytes of *Cyathea* is similar to that of *Hymenophyllopsis*. Further, the earliest leaves of young sporophytes of typical *Cyathea* commonly have photosynthetic epidermal cells with numerous chloroplasts, again resembling *Hymenophyllopsis* and differing from the adult plants of typical *Cyathea*. Young sporophyte leaves are also similar to *Hymenophyllopsis* in the patterns of dissection of the blade into linear single-vein lobes. However, even the youngest sporophytes of *Cyathea* do have stomata, unlike *Hymenophyllopsis*. In many ways, therefore, the anatomy of leaves of young sporophytes of *Cyathea* is similar to the anatomy of leaves of mature adult *Hymenophyllopsis* leaves (Fig. 3A, 3B, 3D).

Hymenophyllopsis as paedomorphic Cyathea species.—Heterochrony has been proposed as an important mechanism affecting the morphological evolution of plants, including pteridophytes (e.g., Guerrant 1988, Pryer and Hearn, 2009).

In his nomenclatural revision of *Hymenophyllopsis* as *Cyathea* species, Christenhusz (2009) suggested that "The reduced height and finely dissected leaves of *Hymenophyllopsis*, in comparison to most *Cyathea*, is probably a result of pedomorphosis." We agree completely, and point out that the heterochrony involved in the origin of *Hymenophyllopsis* goes far beyond simple changes in stature and leaf dissection. Anatomically, *Hymenophyllopsis* should in fact be viewed as precociously fertile, permanent "young sporophytes". The retention of numerous young sporophyte characteristics of *Cyathea* species in adult plants of *Hymenophyllopsis* provides a remarkable example of paedomorphosis playing an important role in the origin of a very distinctive group of species (Fig. 7A, B).

Histologically, *Hymenophyllopsis* species appear to be arrested at an even earlier young sporophyte stage, compared to that expected for their size and stelar anatomy. *Cyathea* specimens with similar stem diameter and stelar complexity to large individuals of *Hymenophyllopsis* species tend to show the presence of stelar sclerenchyma sheaths, secretory cells, aerophores, and abscission plates, all of which are lacking in *Hymenophyllopsis*.

It is arguable whether this *Hymenophyllopsis* example is better seen as neoteny (the retention of juvenile morphological traits in sexually mature adults), or as progenesis (accelerated onset of reproduction in small juvenile organisms). A case can be made that it is most probably a combination of both phenomena: *Hymenophyllopsis* plants do become fertile at a very small size and young age compared to typical *Cyathea*, but even the largest fully mature *Hymenophyllopsis* plants never develop the anatomy that that is characteristic of mature plants of typical *Cyathea* species.

Unique features of *Hymenophyllopsis* not strictly attributable to paedomorphosis include the "filmy" leaves that lack stomata, and the distinctively modified sori appearing to be marginal with bivalved indusia. This last feature is obviously not related to young sporophyte characters, but is perhaps related to the formation of sori on much more finely dissected leaf blades. It should be noted that *Hymenophyllopsis* sori are rather similar to those of *Cyathea akawaiorum*, which grows on Mt. Roraima in the Guyana Highland near where *Hymenophyllopsis* grows (Holttum and Edwards, 1982: Fig. 2, p. 176; Plate #7, Fig. 4).

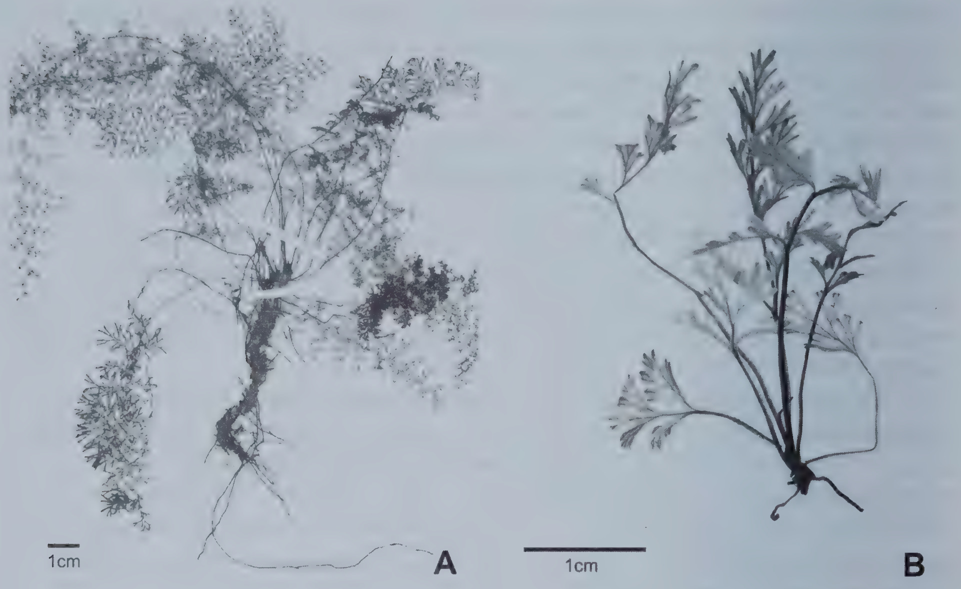

FIG. 7. Adult *Hymenophyllopsis* and young sporophyte of typical *Cyathea*. (A) *H. hymenophylloides* (Maguire 32895, DUKE). A large mature specimen; apart from being fertile at this stage, it retains the basic morphology and simple anatomy of much smaller early young sporophytes of typical *Cyathea*, such as this young specimen of (B) *Cyathea stipularis* (White 1973021, DUKE).

It is striking that even though the vegetative and soral morphology of *Hymenophyllopsis* species is so drastically modified, the sporangia and spores remain essentially identical to those of other species of Cyatheaceae. Despite the diminutive size of the plants themselves, *Hymenophyllopsis* sporangia and spores are not at all reduced; they are larger than those of many *Cyathea* species.

The presence of 32 spores per sporangium in five of the eight *Hymenophyllopsis* shows remarkable variability in such a small group of species. Most Cyatheaceae share the primitive number of 64 spores, but 16 spores is characteristic of *Alsophila* spp. and *Cyathea parvula*, and 32 spores has previously been reported in a few *Cyathea* species (e.g., Gastony, 1974; Gastony and Tryon, 1976).

The *Hymenophyllopsis* species group is remarkable in that it shows the evolution of plants with apparently typical marginal sori from ancestors with superficial sori. This represents an apparent reversal of Bower's (1913) "phyletic slide" from marginal sori to superficial sori. Similar "reverse phyletic slides" have been described for other fern groups (e.g., Wagner, 1953).

The key evolutionary changes in the origin of *Hymenophyllopsis* from typical *Cyathea* will have involved physiological changes to a "filmy fern" leaf anatomy and life style, along with the paedomorphic changes to becoming a "permanent young sporophyte" in both size and stem anatomy. Although there have been previous descriptions of "...a juvenile form of sporophyte with precocious fertility" (e.g., Goebel, 1924; Bower, 1928) and neoteny has been invoked in the evolution of leaf form (Pryer and Hearn, 2009), this current example of neoteny in tree ferns is arguably among the clearest examples of heterochrony known among pteridophytes. It illustrates that paedomorphosis can produce dramatic morphological changes, to the extent that the relationship of *Hymenophyllopsis* to *Cyathea* was obscured until molecular phylogenetic methods were applied.

Future prospects.—Anatomically and morphologically, there are no clear sub-groups within *Hymenophyllopsis*. Arguably, no *Hymenophyllopsis* species is clearly more primitive than any of the others. *Hymenophyllopsis superba* is the only one that retains four petiolar bundles and double pinna trace vascularization, but its small sori and delicate lamina segments seem derived. *Hymenophyllopsis ctenitoides* and *H. universitatis* sori tend to more closely approach the possibly ancestral hemitelioid sorus of many typical *Cyathea* species, but in other features these species seem no closer to typical *Cyathea* than the others. Future molecular studies to clarify relationships among the species may reveal morphological evolutionary trends within the group. Although *Hymenophyllopsis* is currently relatively isolated within New World *Cyathea*, molecular studies may recognize specific extant *Cyathea* species as their nearest living relatives, and help identify the specific genetic changes that would have been involved in this impressive example of heterochrony.

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